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Environmental and Biological Controls on the Geochemistry ($\delta^{18}O$, $\delta^{13}C$, Mg/Ca, and Sr/Ca) of Living Ostracods from Lake Geneva

THESE DE DOCTORAT

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par

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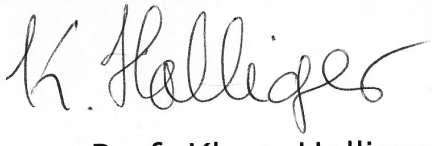

Prof. Klaus Holliger

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Abstract

Ostracods are benthic microcrustaceans enclosed in low-Mg calcite bivalves. Stable isotope compositions, Mg/Ca, and Sr/Ca ratios of ostracod fossil valves have proven useful to reconstruct past environmental conditions. Yet, several discrepancies persist and the influence of many factors remains unclear. It is the aim of this study to improve the use of ostracod valve geochemistry as palaeoenvironmental proxies by examining the extent of isotope fractionation and trace element partitioning during valve calcification. To achieve this, the environmental parameters (pH, temperature) and chemical composition of water (C- and O-isotope composition and calcium, magnesium, and strontium content) were measured at sites where living ostracods were sampled. The sampling was on a monthly basis over the course of one year at five different water depths (2, 5, 13, 33, and 70 m) in Lake Geneva, Switzerland.

The one-year sampling enabled collection of environmental data for bottom and interstitial pore water. In littoral to sublittoral zones, C-isotope composition of DIC and the Mg/Ca and Sr/Ca ratios of water are found to vary concomitantly with water temperature. This is due to the precipitation of calcite, which is induced by higher photosynthetic activity as temperature and/or solar radiation intensify in summer. In deeper zones, environmental parameters remain largely constant throughout the year. Variations of pH, DIC concentrations and C-isotope compositions in interstitial water result from aerobic as well as anaerobic respiration, calcite dissolution and methanogenesis.

Bathymetric distribution, life cycles, and habitats were derived for 15 ostracod species and are predominantly related to water temperature and sediment texture. O-isotope compositions of ostracod valves in Lake Geneva reflect that of water and temperature. However, offsets of up to 3 permil are observed in comparison with proposed inorganic calcite precipitation equilibrium composition. Deprotonation of HCO_3^- and/or salt effect at crystallisation sites may explain the disequilibrium observed for O-isotopic compositions.

C-isotope compositions of ostracod valves are not as well constrained and appear to be controlled by a complex interaction between habitat preferences and seasonal as well as spatial variations of the DIC isotope composition. For infaunal forms, C-isotope compositions reflect mainly the variation of DIC isotope composition in interstitial pore waters. For epifaunal forms, C-isotope compositions reflect the seasonal variation of DIC isotope compositions. C-isotope compositions of ostracod valves is at equilibrium with DIC except for a small number of species (*L. inopinata*, *L. sanctipatricii* and possibly *C. ophtalmica*, and *I. beauchampi*).

Trace element uptake differs considerably from species to species. For most epifaunal forms, trace element content follows the seasonal cycle, recording temperature increases and/or variations of Mg/Ca and Sr/Ca ratios of water. In contrast, infaunal forms are predominantly related to sediment pore water chemistry.

Résumé en Français

Les ostracodes sont de petits crustacés benthiques qui possèdent une coquille faite de calcite à faible teneur en magnésium. La composition isotopique et les rapports Mg/Ca et Sr/Ca d'ostracodes fossiles ont été utilisés maintes fois avec succès pour effectuer des reconstructions paléoenvironnementales. Néanmoins, certains désaccords persistent sur l'interprétation de ces données. De plus, l'influence de certains facteurs pouvant biaiser le signal reste encore inconnue. Ainsi, le but de cette étude est de rendre plus performant l'emploi de la composition géochimique des ostracodes comme indicateur paléoenvironnemental. Pour réaliser cela, cinq sites situés dans le Léman à 2, 5, 13, 33 et 70 m de profondeur ont été choisis pour effectuer les échantillonnages. Chaque site a été visité une fois par mois durant une année. Les différents paramètres environnementaux (pH, température) ainsi que la composition géochimique de l'eau (composition isotopique de l'oxygène et du carbone ainsi que teneur en calcium, magnésium et strontium) ont été déterminés pour chaque campagne. Des ostracodes vivants ont été récoltés au cinq sites en même temps que les échantillons d'eau.

Ce travail de terrain a permis de caractériser la géochimie de l'eau se trouvant juste au-dessus des sédiments ainsi que celle de l'eau se trouvant dans les interstices du sédiment. Dans les zones littorales à sublittorales, la composition isotopique du carbone inorganique dissout (CID) ainsi que les rapports Mg/Ca et Sr/Ca de l'eau varient linéairement avec la température. Ceci peut être expliqué par la précipitation de calcite qui est contrôlée par l'activité photosynthétique, variant elle même linéairement avec la température. Dans les zones plus profondes, les paramètres environnementaux restent relativement constants tout au long de l'année. Les variations du pH, de la concentration et de la composition isotopique du CID dans les sédiments résultent de la libération de carbone engendrée par la dégradation de la matière organique avec présence d'oxygène ou via réduction de nitrates et de sulfates, par la dissolution de carbonates, ainsi que par la méthanogenèse.

La distribution bathymétrique, le cycle de vie ainsi que l'habitat de 15 espèces ont été déterminés. Ceux-ci sont principalement reliés à la température de l'eau et à la texture des sédiments. La composition isotopique de l'oxygène des valves d'ostracodes reflète celle de l'eau et la température qui régnait lors de la calcification. Néanmoins, des écarts pouvant aller jusqu'à 3 ‰ par rapport à l'équilibre théorique ont été obtenus. La déprotonation de HCO_3^- ou un 'effet de sel' pourrait être à l'origine du déséquilibre observé.

La composition isotopique du carbone des valves d'ostracodes n'est pas aussi bien cernée. Celle-ci semble être principalement contrôlée par une interaction complexe entre l'habitat des ostracodes et les variations saisonnières et spatiales de la composition isotopique du CID. Pour les espèces endofaunes, la composition isotopique du carbone reflète principalement la variation de la composition isotopique du CID à l'intérieur des sédiments. Pour les formes épifaunes, c'est la variation saisonnière de la composition du CID qui contrôle celle de la coquille des ostracodes. En général, la composition isotopique du carbone des valves d'ostracodes est en équilibre avec celle de CID, hormis pour quelques rares espèces (*L. inopinata*, *L. sanctipatricii* et peut-être *C. ophtalmica* et *I. beauchampi*).

L'incorporation des éléments traces diffère passablement d'une espèce à l'autre. Pour la plupart des espèces épifaunes, la teneur en éléments traces des coquilles reflète les variations saisonnières. Ces espèces semblent enregistrer les variations soit de la température soit des rapports Mg/Ca et Sr/Ca de l'eau. La teneur en élément traces des formes infaunales, au contraire, est principalement reliée à la chimie de l'eau interstitielle.

Résumé Grand-Public

La connaissance de l'évolution du climat dans le futur est primordiale pour notre société, car elle permet de développer différentes stratégies pour faire face aux problèmes engendrés pas le changement climatique : stratégies environnementale, humanitaire, ou encore économique. Cette problématique est actuellement, à juste titre, sujet d'une vive préoccupation.

La géologie peut-elle contribuer à l'effort communautaire entrepris? Naturellement, ce sont les climatologues qui sont sur le devant de la scène. Il n'empêche que ces derniers, pour pouvoir prédire l'avenir, doivent s'appuyer sur le passé. La géologie est alors d'un grand intérêt car c'est effectivement la seule science qui permette d'estimer les variations climatiques à grande échelle sur de longues périodes. Ainsi, voulant moi-même contribuer aux recherches menées dans ce domaine, je me suis tourné à la fin de mes études vers la paléoclimatologie, science qui a pour but de reconstruire le climat des temps anciens. Nous nous sommes rendu compte que l'évolution climatique de la région où nous habitons n'avait pas encore fait le sujet d'études approfondies. Il est pourtant important de connaître la variation locale des changements climatiques pour obtenir des modèles climatiques fiables. En conséquence, un vaste projet a vu le jour : reconstruire, à l'aide des sédiments du lac Léman, les variations paléo-climatiques et paléo-environnementales depuis le retrait du Glacier de Rhône, il y a environ 15'000 ans, jusqu'à nos jours.

Pour ce genre de travail, la géochimie, qui est une forme de chimie utilisée en science de la terre regroupant la chimie classique et la chimie isotopique, est une alliée particulièrement efficace. Elle permet en effet, via différentes mesures faites sur des archives géologiques (par exemple des fossiles ou des sédiments) d'obtenir des informations, souvent quantitatives, sur les conditions (le climat, la flore ou encore la bio productivité, etc…) qui régnaient il y a fort longtemps. Les coquilles d'ostracodes, qui sont de petits animaux vivant au fond des lacs, sont une des archives les plus prometteuses.

Ces animaux sont des petits crustacés s'entourant d'une coquille calcaire qu'ils sécrètent eux-mêmes. A la mort de l'animal, la coquille est intégrée dans les sédiments et reste intacte à travers les âges. Des études ont montré qu'en analysant la géochimie de ces coquilles fossiles, il est possible de reconstruire les conditions environnementales qui régnaient à l'époque de vie de ces fossiles. Cette démarche nécessite qu'une condition bien précise soit remplie: la composition géochimique de la coquille doit enregistrer de manière fidèle la chimie de l'eau et/ou la température de l'eau présentes au moment de la sécrétion de la coquille.

Le but spécifique de notre recherche a précisément été d'étudier la façon dont la chimie de l'eau ainsi que sa température sont enregistrées dans la coquille des ostracodes. Une fois les relations entre ces divers paramètres dans l'étant actuel du système établies, il sera alors possible de les utiliser pour interpréter des données issues de coquilles *fossiles*. Pour ce faire, nous avons mesuré la température de l'eau de manière continue et récolté mensuellement des échantillons d'eau et des ostracodes *vivants* pendant une année. Cinq sites situés à 2, 5, 13, 33 et 70 mètres de profondeur ont été choisis pour effectuer ces échantillonnages dans le Léman.

Le travail de terrain nous a amené à étudier la biologie de 15 espèces. Nous avons pu établir la profondeur à laquelle vivent ces animaux, leur période de développement ainsi que leur habitat respectifs. Ces résultats ont permis de mieux cerner la relation qu'il existe entre la chimie de l'eau, sa température et la composition géochimique des coquilles d'ostracodes. Nous avons ainsi pu confirmer que les coquilles d'ostracodes enregistrent de manière fidèle la composition chimique et isotopique de l'eau. De même, nous avons pu établir de manière plus précise l'effet de la température sur la géochimie des coquilles. Néanmoins, les relations trouvées entre ces trois éléments sont plus complexes pour certaines espèces, cette complexité étant souvent liée à un caractère spécifique de leur écologie. Nous avons mis en lumière certains effets qui biaisent les résultats et défini précisément les conditions dans lesquelles on peut s'attendre à avoir des difficultés dans leur interprétation.

Maintenant que nous avons établi les relations entre le climat actuel et la composition géochimique des coquilles d'ostracodes actuels, nous pouvons, sur la base de ce modèle, reconstruire le climat depuis le retrait du Glacier du Rhône jusqu'à nos jours à l'aide d'ostracodes fossiles. Mais cela est une autre histoire et fera, je l'espère, le sujet de nos futures recherches.

Chapter I :

INTRODUCTION

1. General Introduction

Ostracods are small microcrustaceans that colonize almost all types of aquatic environments. Their carapace consists of two dorsally articulated valves, which in most groups, and in all freshwater species, are mineralised with low magnesium calcite (Kesling, 1951; Sohn, 1958). Like other crustaceans, the ostracods develop by successive moulting (ecdysis). Freshwater ostracods have usually nine free living stages separated by eight moults, the ninth stage being the adult. Only the last stage (the adult) is fully formed and sexually mature, but all development stages possess a more or less calcified cuticle. At each moult, the carapace is discarded and a new one is rapidly calcified. Most ostracods are benthic forms that either crawl on the surface of the sediment ('epifaunal' forms) or dig into the sediment interstices ('infaunal' forms).

Ostracod fossil valves are numerous in sediments and often well-preserved thanks to the chitin membranes that surround the calcite (Oertli, 1975). Ostracods are, therefore, excellent organisms for paleontological studies. Since some species present very restricted environmental needs, fossil assemblages can be used to reconstruct palaeoenvironmental conditions (Carbonel et al., 1988; Löffler, 1997). On the base of modern assemblages datasets and 'canonical correspondence analyses', the ostracodologists are even able to reconstruct quantitatively several environmental parameters such as temperature, water chemistry, water velocity (Curry, 1999; Mezquita et al, 2005; Viehberg, 2006; Yilmaz and Külköylüoğlu, 2006; Mischke et al., 2007, 2008a), or the range in air temperature (Horne, 2007). Besides, some authors paid more attention to the morphology of the valves and developed morphometric tools to reconstruct past water temperature (Kamiya, 1988; Cronin et al., 2005) or past water salinity (Rosenfeld and Vesper, 1976; Keatings et al., 2007).

In addition, the calcite of the ostracod carapace can be used as a geochemical archive. In closed basins, oxygen isotope compositions and trace element contents allow the estimation of past precipitation/evaporation ratio (Engstrom and Nelson, 1991; Chivas et al., 1993; Curtis and Hodell, 1993; Yu et al., 2002). In open freshwater deep lakes, oxygen isotope compositions may provide information on air temperature (Lister, 1988; Schwalb et al., 1994, von Grafenstein et al., 1999a). When the Mg/Ca ratio of water is constant, magnesium content of ostracod valves can also be used as palaeothermometer (Dwyer et al., 1995, 2002).

Although these methods have proven useful for palaeoenvironmental reconstructions, many local characteristics may bias the recorded signal. It is, therefore, necessary to comprehend the functioning of the whole system to be able to interpret correctly the geological archives. The growing attention paid to the actual global change leads the scientists to constrain in more detail how fast and to which extent global and local conditions can change. Thus, very detailed and reliable palaeoenvironmental reconstructions are urgently needed. To attain this, the geologists are continuously developing new methods, pushing years after years the cutting edge in the field of palaeoenvironmental reconstruction. The actual demand for sensibility and reliability of past environmental reconstructions requires knowledge on the precision of the parameters recorded and what may disturb such composition. One of the best manners to achieve this is to calibrate the system before attempting to use the different proxies to reconstruct past conditions. The necessity of such studies has recently been recognised. Many authors investigated how the specific system they study operates in the present in the aim to better constrain the interpretation deduced from the sedimentary archives. This was intensely undertaken in the field of ostracodology, in part because of the ubiquitous occurrence of these organisms, the availability of modern analogue, as well as the quality of the fossil preservation. Such 'actualistic' studies consist habitually of two steps. The first one aims to assess the incorporation of host water physico-chemical parameters (T°, water chemistry and isotopic composition, etc…) in ostracod shells, comparing the geochemistry of living ostracods with the environmental dataset (Chivas, 1983, 1986; Engstrom and Nelson, 1991; Dwyer et

al., 1995; Heaton et al., 1995; Xia et al., 1997; De Deckker et al., 1999; von Grafenstein et al., 1999b, Wansard and Mezquita, 2001; Palacios-Fest and Dettman, 2001; Chivas et al., 2002; Keatings et al., 2002a; Cronin et al., 2005; Kondo et al., 2005). The second step seeks to evaluate how the system reacts to environmental changes, comparing the geochemistry of fossil ostracod shells with historical measurements (Engstrom and Nelson, 1991; von Grafenstein et al., 1996, Keatings et al., 2007; Lawrence et al., 2008).

Lake Geneva, because of its large catchment area and large size, offers the opportunity to study past environmental changes in Western Switzerland since the last deglaciation. Its location in Central Europe, at the external angle formed by the southern and the eastern branches of the Alps, is particularly interesting for investigations of how the presence of a major mountain belt affects global and local climate changes. Despite the importance of this lake as Central Europe largest lake (in volume), few studies have concentrated on its palaeoenvironmental evolution. Last studies to this date used sedimentary structures to reconstruct retreat of the Rhone Glacier as well as wind pattern during the Holocene (Moscariello et al., 1996; Girardclos et al., 2003, 2005; Baster et al., 2003). In addition, the isotopic and trace element contents of gastropod opercula and ostracod shells have been investigated by Anadón and co-authors in 2006. These authors demonstrated that these fossils are valuable tools to reconstruct past climatic condition in Western Switzerland. However, the sediment cores used for their study were retrieved in littoral zones. Such positioning leads to several difficulties in reconstructing past environment evolution. First of all, the sedimentary record suffers of a low temporal resolution and non-continuous sedimentation. The evolution of water oxygen isotope composition recorded in ostracod shells might be disturbed since water temperature varies intensely on long and short term in such shallow areas. Beside, the study used the vital offset (see below for a definition of the vital offset) determined by von Grafenstein and co-authors (1999b) to interpret the oxygen isotope composition of *Candona neglecta* shells. At the time of the study, it was considered that vital offsets do not vary from one location to the other. However, preliminary results obtained during a master thesis carried out at the University of Lausanne showed that in Lake Geneva the vital offsets were much higher than those determined by von Grafenstein and co-authors (1999b), pointing toward probable variation of the vital offset from one location to the other (Decrouy, 2004). Finally, Anadón and co-authors (2006) assumed on the basis of Meisch (2000) and the reference within, that *Candona neglecta* reaches maturity in late spring and fall and that the shell they analysed calcified during this period, i.e. the warmest period of the year. Life cycle of *Candona neglecta* in Lake Geneva has not been investigated until the present study. Furthermore, data from the literature suggests that this species might actually reach maturity during the coldest period of the year in shallow water and not the warmest one (Hiller, 1972). Hence, given the importance of the present debates on climate change and the lack of high-resolution palaeoenvironmental reconstructions in the region, a continuous sedimentary record from Lake Geneva and examination of past environmental evolution since deglaciation, may well help to provide such needed reconstructions. Ostracods are an obvious first choice for such studies.

Driven the above, the aim of this study is to reconstruct the palaeoenvironmental conditions for Western Switzerland using the sedimentary record of Lake Geneva. As a first step, the present system has to be studied in order to get a solid basis before attempting to interpret fossil archives. The focus was, therefore, put on the incorporation of the different environmental conditions in ostracod valves. The results of the present study will form the basis for future work on palaeoenvironmental reconstruction within Lake Geneva. In addition, there is hope that the results will shed some light on biomineralisation processes in ostracods as well as isotopic and chemical equilibration found for these organisms.

2. State of the Art

2.1. Ostracod Valve Struture

Biomineralisation in ostracods has not been as intensely studied as in other organisms such as foraminifera, corals, isopods, etc. (Cohen and McConnaughey, 2003; Erez, 2003; Ziegler, 2008). However, examinations of valve structure and biomineralisation processes effectuated by several authors allow us to describe the different stages encountered during moulting.

Figure 1.1 presents a cross section of the general structure of an ostracod and the organization of the soft body and the calcified carapace. The cuticle consists of a calcified outer lamella and an inner lamella. The latter is only calcified at the margin of the valve. This calcified part of the inner lamella is

named ‘duplicature’. Figure 1.2 shows an enlargement of the cuticle boxed in Figure 1.1. The figure presents a synthetic model of the ostracod cuticle structure. The drawing is based on the observations effectuated on *Cypridopsis vidua* (Bate and East, 1972) and *Bicornucythere bisanensis* (Okada, 1982). Apart from calcite, the carapace of ostracods contains approximately 2 to 15 % of chitin and protein (Sohn, 1958). The outer lamella consists of a succession of layers. The following description is from the outside to the inside. The epicuticle is the first layer. Its ultrastructure presents a succession of three layers. Ostracod epicuticle appears to correspond to that of other arthropods and must, therefore, be composed of lipids, polyphenols, and proteins as in the larger crustacea (Bate and East, 1972, 1975; Okada, 1982). The epicuticle separates the ostracod from the external environment and must act as chemical barrier. Under the epicuticle, we find the calcified part of the carapace. In ostracods, the calcite minerals are enclosed in chitin membranes (Jørgsen, 1970). The organisation of the chitin and the calcite minerals varies among the different taxonomic groups. The chitin framework can show a parabolic pattern as in *Cypridopsis vidua* (Cyprididae), *Eucypris lutaria* (Cyprididae), and *Eucypris virens* (Bate and East, 1975; Rosenfeld, 1979), an interlocking lattice structure of chitin fibres (Bate and East, 1975), irregular space lattice structure of chitin fibres (Langer, 1973), or a piled membrane structure as in *Bicornucythere bisanensis* (Cytheroidea) and other specimen of the same Superfamily (Okada, 1982). The calcified layer can present two distinct structures. In Cypridoidea, two layers are distinguishable: the exocuticle and the endocuticle. In contrast, only one layer is observed in Cytheroidea and is then called procuticle. The first case is illustrated in Figure 1.2. We find successively the epicuticle, the exocuticle, and the endocuticle. This structure is typical for decapod crustacea (shrimps or crabs, for examples). The main difference between exo- and endocuticle is the density of the chitin framework: in the exocuticle, the chitin fibres are tightly packed whereas the endocuticle have a much more open structure, the chitin fibres being more slender and the space between being considerably larger (Bate and East, 1972). In the case of the procuticle found in Cytheroidea, the shell is almost completely built of calcite crystals (Keyser and Walter, 2004) and the organic framework is composed of membranes (Okada, 1982).

Under the cuticle, a membranous layer separates the calcified part of the carapace from the underlying epidermal cells. The epidermis, strictly speaking, consists of two layers of cells. The first one consists of outer epidermal cells lying just under the cuticle.

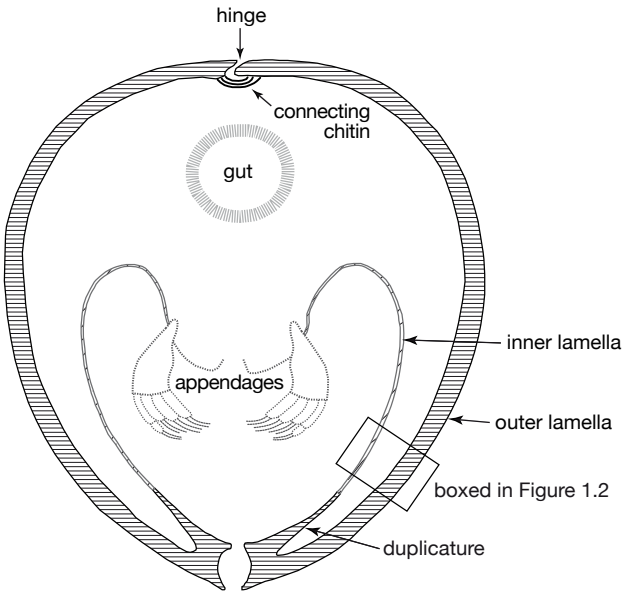


FIGURE 1.1
Cross-section of an ostracod showing the location of the outer lamella, the duplicature, and the inner lamella (from Bate and East, 1972).

This layer belongs to the outer lamella. The second layer consists of the inner epidermal cells and lines the inner cuticle. These cells belong to the outer lamella. Epidermal cells contain many granules of approximately 1 µm diameter. Different internal structures of granule can be observed (Rosenfeld, 1979; Okada, 1982). The granules are distributed within outer and inner cells (Okada, 1982) and form a more or less dense continuous layer lining the calcareous valve (Rosenfeld, 1979, Keyser and Walter, 2004). These authors suggest that the granules play a first order role in valve calcification (see below). Mitochondria are particularly numerous in inner epidermal cells. Since ostracods have generally no blood vessels or distinct hemocoel, oxygen uptake must be performed by the cells through the thin inner lamella cuticle (Okada, 1982).

Subdermal cells are located in the space found between outer and inner epidermal cell layers. These cells are often amoeboid and contain granules in rough-surfaced endoplasmic reticulum (r-ER). Abundant r-ER in subdermal cells indicates extremely high activity of protein synthesis (Okada, 1982). Granules may therefore be formed in subdermal cells. In addition, these cells can migrate (Rome, 1947) and may transport nourishment to the fixed cells (Okada, 1982).

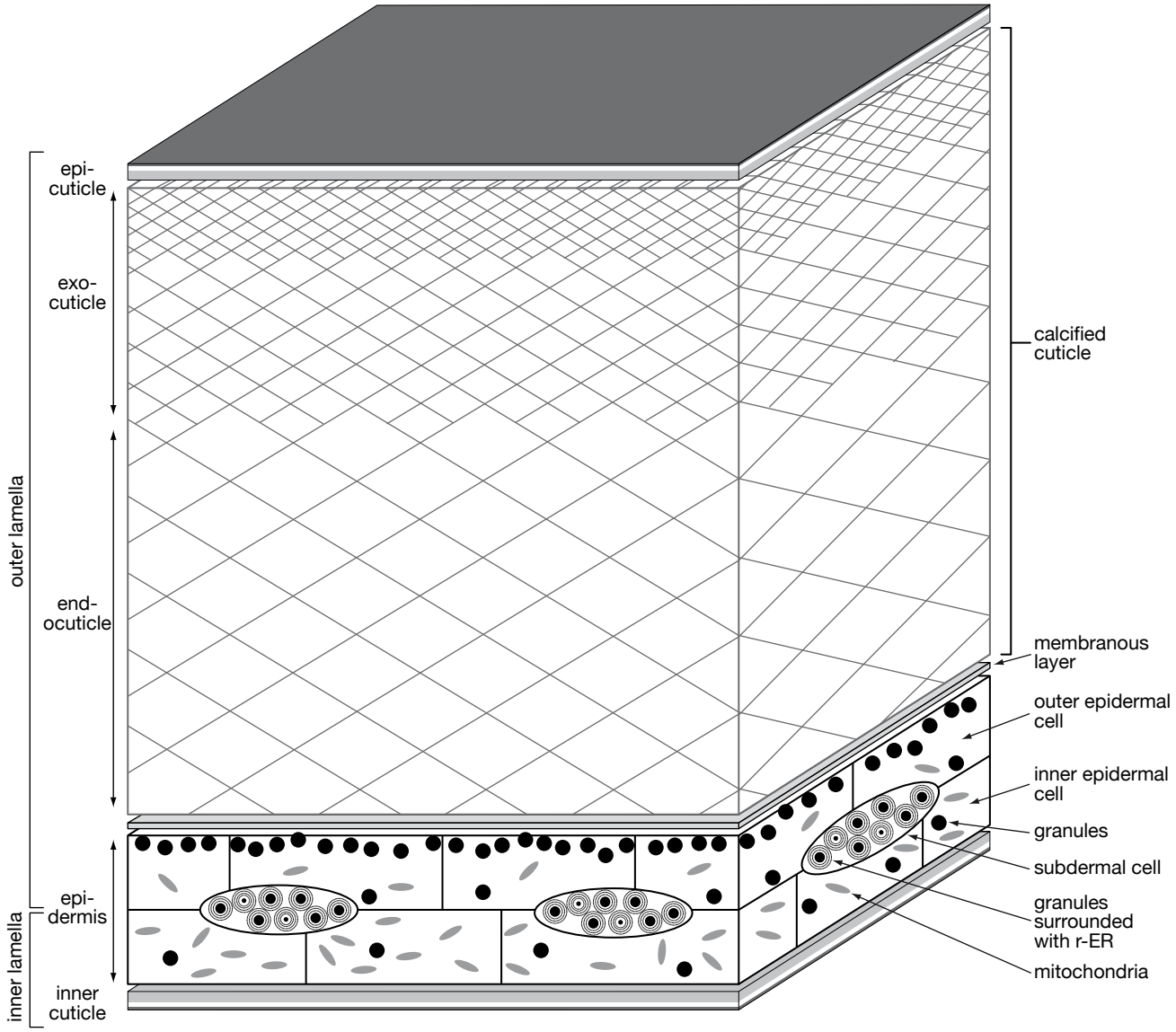


FIGURE 1.2
Structure of the cuticle boxed in Figure 1.1 (modified after Bate and East, 1972 and Okada, 1981).

2.2. Biomineralisation in Ostracods

Figure 1.3 presents the different steps observed during moulting. This model compiles various observations effectuated by different authors (Turpen and Angel, 1971; Rosenfeld, 1979; Okada, 1982; Chivas et al., 1983, 1986; Keyser and Walter, 2004; Morishita et al., 2007). The moulting process can be divided into 12 stages (A to L). The first one is the fully calcified juvenile valve (A), the last one the fully calcified adult valve (L). Stages B to G plus L are mainly based on the observations by Okada (1982), stages A plus H to K on Keyser and Walter (2004). The cuticle formation is described below stage by stage.

(A) Many granules and amorphous granular material is observed in the calcified cuticle of juveniles (Rosenfeld, 1979; Keyser and Walter, 2004). Apart of these particularities, the carapace structure is similar to that described in the subsection 2.1 of the present chapter.

(B) Required for moulting is the separation of the old outer cuticle from the body of the animal in order to produce the new one underneath the old one. This is achieved by a partial break down of the membranous layer lining under the old outer cuticle and the intrusion of ecdysial fluid between the old outer cuticle and the epidermis. The old outer cuticle is attached to the

body of the animal with supporting fibres that act as anchors (Okada, 1982).

(C) After this, the new outer epicuticle is progressively produced. In stage C, cuticular fragments form a non-continuous, thin layer (Okada, 1982).

(D) In the following stage, the new outer epicuticle is completed and is similar to the epicuticle of completed calcified valves (Okada, 1982).

(E) Once the new outer epicuticle is formed, many minute granules of two types – those about 5 nm and those about 50 nm in diameter – can be observed in the space between the epidermis and the outer epicuticle. Extremely thin membranes can also be observed. These probably form the chitin framework at later stages. For Cytheroidea, the outer cuticle is, at this stage, formed of an outer epicuticle and a procuticle (Okada, 1982).

(F) Just after ecdysis (moulting), the new outer cuticle is exposed to water and the procuticle swells (Okada, 1982).

In addition, the following can be pointed out at this stage:

– The granules are particularly abundant in the outer epidermal layer during moulting (Rosenfeld, 1979; Keyser and Walter, 2004).

– Exocytosis of the granules of epidermal cells are frequently observed throughout the moulting (Fig. 1.3 E) These exocytosis are not restricted to the calcification period after ecdysis. This suggests that epidermal cells supply various organic materials to form the cuticle by secreting granules (Okada, 1982). These granules were actually assigned a more particular major role in cuticle calcification by several authors (Rosenfeld, 1979; Keyser and Walter, 2004).

– Turpen and Angel (1971) observed that the position of amoeboid subdermal cells within the epidermis appears to change so they are found concentrated in the area being calcified. In the early stages of calcification they are concentrated at the margin of the valve, and, as these portions are calcified, they move in towards the centre, which is the last part of the valve to be calcified.

– In the same study, the authors demonstrated, using ^{45}Ca labelling, that calcium used for the formation of the shells is taken directly from the water without build up or storage of calcium within the body of the animal prior to the moult. Still, the conclusion of Turpen and Angel (1971) has been questioned by numerous authors (Keatings, 1999; Palacios-Fest and Dettman, 2001; Dettman et al., 2002; Keyser and Walter, 2004).

– Chivas and co-workers (1983, 1986) observed that non-completely calcified valves presented very high amounts of magnesium. This was, in contrast, not observed for strontium. Palacios-Fest and Dettman (2001) confirmed that magnesium content of non-completely calcified valve was very high, with the animal coming very close to precipitating magnesite.

Returning to the main points of cuticle formation:

(G) EDX and ESI analyses indicated that the granules of the outer epidermal layer contains compounds of phosphorous and calcium with only small amounts of carbon but interestingly neither magnesium nor strontium. Thus, the granules contain calcium phosphate maybe in the form of apatite (Keyser and Walter, 2004).

(H) The apatite is secreted through the outer epidermal cell membrane in the area beneath the shell. An electron-dense stained area directly at the border of the membrane and the granule has been noted, but whether the secretion is an osmotic or membrane driven process is not yet clear. The material released from the cells gives rise to platelets on the inner surface of the new shell (Keyser and Walter, 2004).

(I) The platelets then lose their distinct form and build groups of very tiny granules of not more than 20 nm in diameter. However, at this stage, the material is already calcium carbonate and might represent amorphous calcium carbonate. Due to its higher solubility, this amorphous material can probably be mobilised by the animal (Keyser and Walter, 2004). High concentration of magnesium in the procuticle, maybe bound to the chitin framework, might permit to prevent crystallisation of amorphous calcite to calcite since presence of magnesium increases the solubility of calcite (Davis et al., 2000). This has been shown to be the case for isopods (Ziegler, 2008).

(J) If the amorphous calcium carbonate remains in the region for a longer period, it will eventually crystallise and produce the typical crystals in the shell of an ostracod (Keyser and Walter, 2004). Based on distributions of strontium and magnesium within the shell and crystallite size, Morishita and co-authors (2007) proposed that the outer part of the cuticle is formed at an earlier stage whereas the inner part of the cuticle might be formed at the later stage of carapace formation.

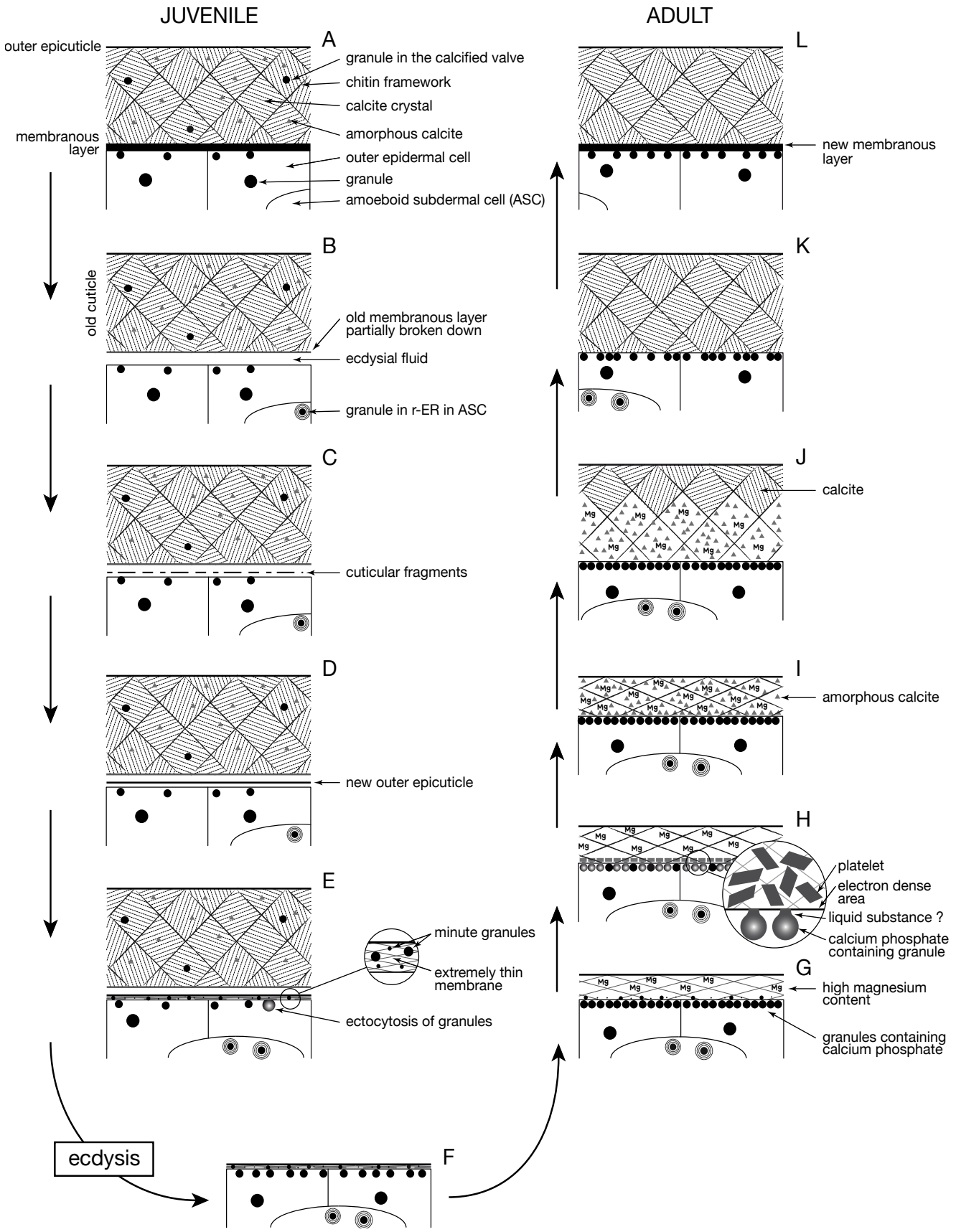


FIGURE 1.3
Biomineralisation in ostracods (modified after Okada, 1982)

(K) At a certain time, the whole cuticle is calcified and has the geochemical composition of a completed carapace, i.e., the magnesium content is stable and represents less than 1% of the entire calcified cuticle.

(L) In the last steps, a new membranous layer is formed, separating the calcified cuticle from the epidermal cells. Note that the calcified cuticle of adults is totally crystallised and presents neither granules nor amorphous material as is the case for cuticle of juveniles.

Since this model is based on observations made on different species, it is possible that some species only exploit some of the processes described here and other species possesses different ones. It is likely that each taxonomic Family possesses its own valve calcification procedure. The differences in structures and geochemical compositions observed among different taxa support this hypothesis. Still, this model permits to grasp some processes that might be implied during ostracod valve calcification.

2.3. Ostracod Valve Geochemistry

2.3.1. Oxygen isotope fractionation

Oxygen isotope fractionation during calcite growth is temperature dependent. During crystallisation, the heavy isotopes are preferentially incorporated in the crystals. As water temperature increases, isotopic fractionation diminishes and the oxygen isotope composition of calcite minerals becomes lower. Experiments to date on synthetic calcite grown in the laboratory permitted to refine the previously published fractionation factors (Kim and O'Neil, 1997). The authors argue that the results obtained in dilute calcium solution represent equilibrium. Knowing the oxygen isotope composition of water and the temperature at which calcite forms, it is possible to predict its oxygen isotope composition, on the basis of the published fractionation factors.

Oxygen isotope compositions of ostracod valves are offset when compared to the predicted isotopic composition of an equilibrium calcite that would have grown under same conditions. This offset is often referred to as the 'vital offset'. Knowledge of this positive offset is important when interpreting oxygen isotope compositions of fossil ostracod valves for past water temperatures or past water oxygen isotope compositions. Von Grafenstein and co-workers (1999b) determined vital offsets for different species using living ostracods collected in two South German lakes. These authors demonstrated that the vital offset is species specific and is temperature independent. The vital offset can, therefore, simply be added to the theoretical value of an equilibrium calcite to get the value for ostracods. In other words, when fossil valves are analysed, the vital offset has to be subtracted from ostracod oxygen isotope compositions before using the fractionation factors established for synthetic calcite to estimate past water temperatures and/or past water isotopic compositions. A few years later, Keatings and co-authors (2002) measured a slightly different vital offset for Candoninae compared to previous values. These authors did not mention nor discuss this discrepancy, maybe because the difference was quite low. However, unpublished studies on oxygen isotope compositions of modern ostracod valves from Lake Geneva reveals that the vital offset might change from one location to the other (Decrouy, 2004). Using vital offsets from the literature in this locality, for example, gives unrealistic results with animals having to moult while temperature was lower than the minimal winter temperature (~ 4°C) and, for some samples, even below 0°C. Thus, the vital offset has to be higher for ostracod inhabiting Lake Geneva. Detailed studies of ostracod oxygen isotope fractionation in Lake Geneva are, therefore, clearly required before attempting to use this proxy for palaeoenvironmental reconstructions.

2.3.2. Carbon isotope fractionation

Carbon isotope fractionation is, for the range of temperature studied, not temperature dependent. The calcite carbon isotope composition is enriched in ^{13}C by approximately one per mil relatively to the isotopic composition of bicarbonate (Romanek et al., 1992). Because bicarbonate is the dominant species at neutral pH, the isotopic composition of a calcite that grew in equilibrium with DIC is expected to be about one per mil higher than that of DIC. However, in alkaline or acidic water, bicarbonate is not the only species present. Hence, the relation between DIC isotopic composition and calcite carbon isotope composition is more complex since the relative amounts and the relative enrichment factors of dissolved carbon dioxide and/or carbonate ions have to be taken in account.

Most of the ostracod taxa investigated until now have carbon isotope compositions that are in equilibrium with those of the DIC (von Grafenstein et al., 1999b; Keatings et al., 2002). However, some species appear to be in disequilibrium with DIC. As the isotopic composition of DIC varies extremely in natural systems, it is often difficult to discern which parameter controls the carbon isotope composition of ostracod valves and whether this one is in equilibrium

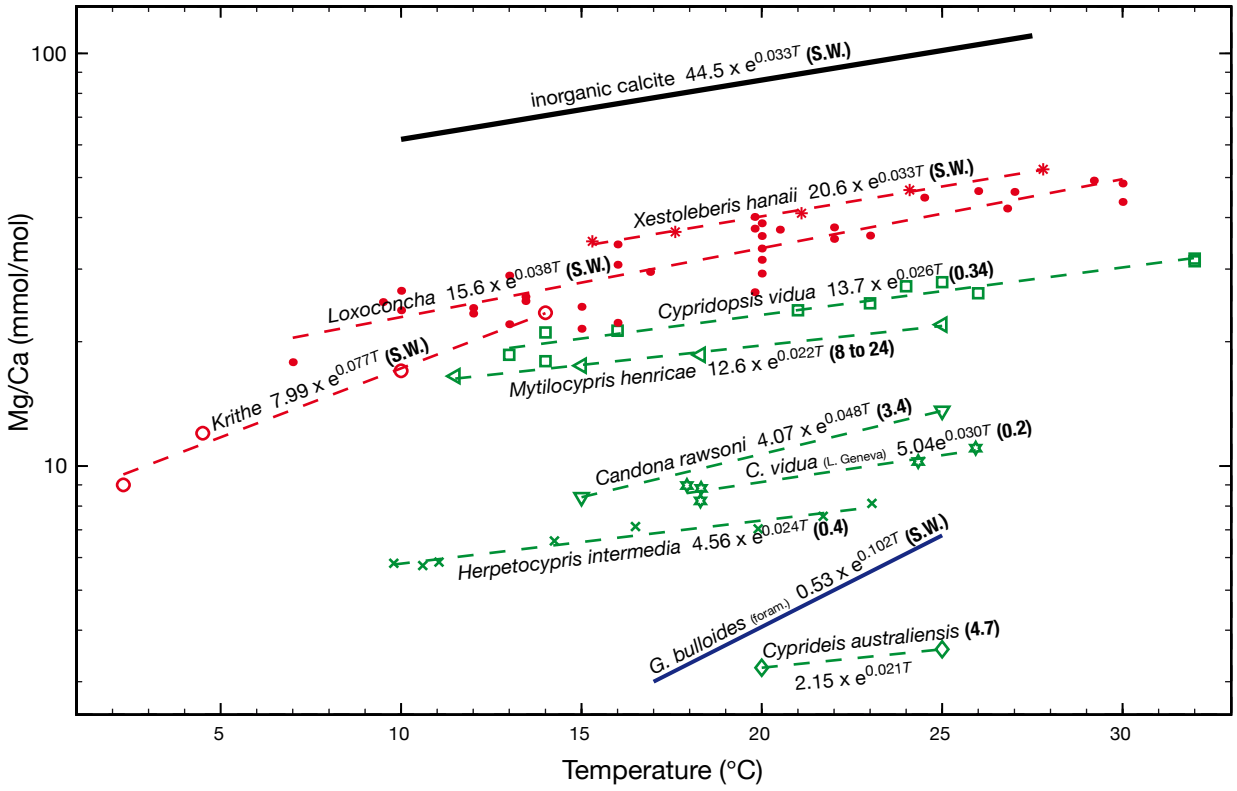


FIGURE 1.4
Relation between Mg/Ca ratios of different types of calcite and temperature (modified after Lea, 2003). Red dashed lines represent marine ostracods, green ones continental ostracods. Bold numbers in brackets stands for Mg/Ca ratio of water, S.W. for seawater.

or not with DIC. Hence, a detailed study of the spatial and temporal variation of DIC isotopic composition is essential to understand how seasonality and microenvironment can affect the carbon isotope composition of ostracod valves.

2.3.3. Magnesium partitioning

Magnesian calcites are predominantly associated with biological processes. Most efforts to understand the partitioning of magnesium in calcite were investigated on calcite of biogenic origin, mainly because of their general availability, and presumably their dominance in natural systems (Mackenzie et al., 1983). More recent studies have focussed on magnesium incorporation into non-biogenic calcite in order to understand the general rules in 'simple' systems and have reinvestigated the biogenic realm afterwards. Because magnesian calcite is dominant in marine organisms as in marine cements, most studies have largely examined marine systems. The incorporation of magnesium into calcite test of marine organism such as foraminifera, corals, coccoliths, etc. (e.g. Lea, 2003; Langer et al., 2006) as well as in synthetic inorganic magnesian calcite precipitates from sea water (Mucci and Morse, 1983, Busenberg and Plummer, 1989) was studied in detail. Both organic and inorganic systems have shown that incorporation of magnesium was higher in water having higher Mg/Ca ratios and of higher temperatures. The incorporation of magnesium into calcite can be described by the following partition coefficient (D_{Mg}):

$$D_{Mg} = Mg/Ca_{Calcite} / Mg/Ca_{water} \quad (1.1)$$

where Mg/Ca is the molar ratio of magnesium and calcium to calcite and in water. Equation (1.1) predicts that for constant D_{Mg}, the incorporation of Mg depends of the Mg/Ca ratio in water. Temperature, together with the composition of water and calcite, pressure and reaction rate, can also affect the partition coefficient (Morse and Bender, 1990). Actually, the substitution of magnesium into calcite is endothermic and is, therefore, favoured at higher temperature. The enthalpy change for the reaction base on thermodynamic data is 21 KJ mol^{-1} (Koziol and Newton, 1995). This corresponds to an exponential increase in Mg/Ca of 3 % per °C (Lea et al., 1999). Growth rate seems to have no effect on Mg partitioning into inorganic calcite (Morse and Bender, 1990; Lopez et al., 2009).

Compared to inorganic calcite precipitated from seawater, marine ostracods are considerably depleted in Mg (Figure 1.4). This is also the case for foraminifera (Lea et al., 1999, Lea, 2003). The reason for this remains unclear but biological processes occurring during test calcification must certainly play an important role. Inorganic magnesian calcite has not been as thoroughly investigated in the continental realm as in the marine one. Still, some studies investigated the Mg content of ostracod valves issued from a broad range of environments from hypersaline lakes to soft water dilute systems. Results from the available literature are plotted in Figure 1.4 together with marine data. An interesting point emerging from this compilation is that no ostracods have higher magnesium content than inorganic calcite precipitated in seawater (Mg/Ca ≈ 5), even ostracods grown in hypersaline lakes with Mg/Ca ratios ranging from 5 to 24 (Chivas et al., 1983; De Deckker et al., 1999). A second interesting point is that there is absolutely no decrease in the Mg content of ostracods with decreasing water Mg/Ca. It appears that the ostracod calcite Mg/Ca ratio remains constant over a certain range of values, independently of water composition. This implies that the partition coefficient for magnesium (D_{Mg}) must be higher in dilute water having low Mg/Ca ratio. In other words, the lower the Mg content in water, the higher is the Mg uptake relative to Ca. This pattern is observed for different continental taxa collected in diverse environments (Figure 1.5 A; Holmes and Chivas, 2002). Inorganic calcites precipitated from a large range of Mg/Ca ratios and theoretical models demonstrate that this pattern is also observed in the inorganic system (Fig 1.5 B: Busenberg and Plummer, 1989). A previous study on Mg incorporation into inorganic calcite observed that above a Mg/Ca ratio of water of 7.5, the concentration of magnesium in the calcite followed a classical thermodynamic behaviour characterized by a constant distribution coefficient of 0.0123. Below a ratio of 7.5, the calcite is, in contrast, enriched in magnesium relative to what is predicted by the constant distribution coefficient. This preferential incorporation might be due to a relative enrichment of adsorbed magnesium onto the surface of the growing mineral (Mucci and Morse, 1983). These results might explain the variation of ostracod D_{Mg}. Still, magnesium must play a major role in ostracod valve calcification (see above; Chivas et al., 1983, 1986, Palacios-Fest and Dettman, 2001) and a simple inorganic model cannot be applied directly to describe magnesium uptake during ostracod valve calcification. A last point of interest emerges from Figure 1.4. On the whole, all ostracods, except the genus *Krithe*, present an exponential increase of approximately 3% in Mg/Ca ratio. This is the thermodependence expected for magnesium incorporation in inorganic

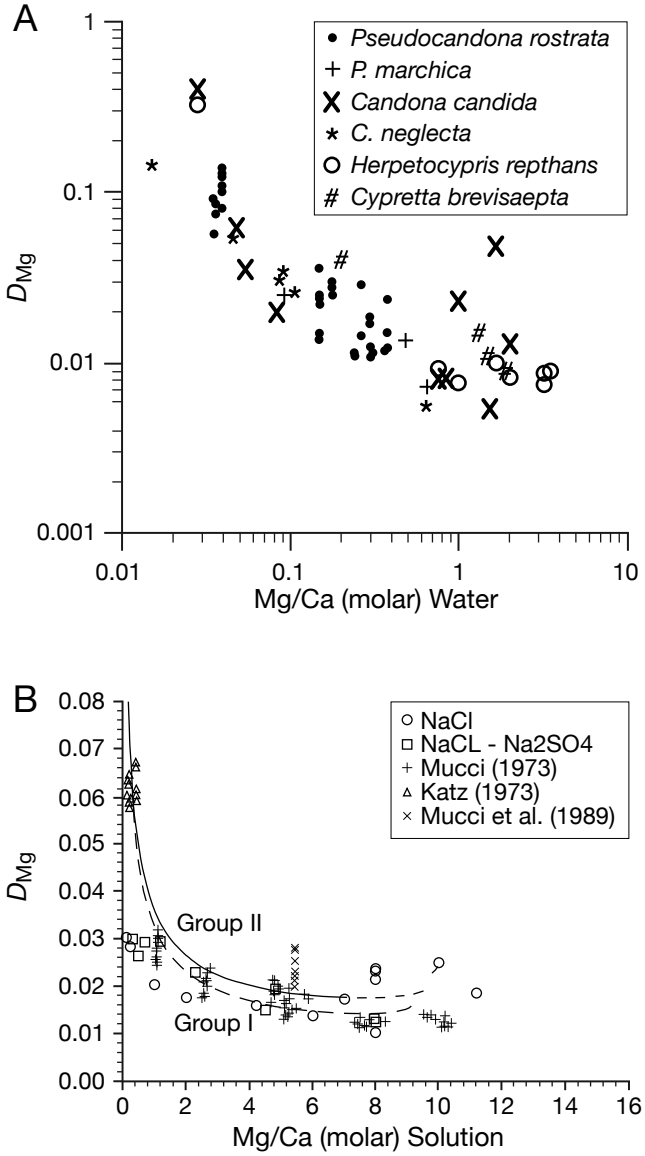


FIGURE 1.5
(A) Relation between partition coefficient for magnesium in ostracod calcite and Mg/Ca ratio of water (from Holmes and Chivas, 2002).
(B) Relation between partition coefficient for magnesium in biogenic and inorganic calcite and Mg/Ca ratio of water (from Busenberg and Plummer, 1989; see original publication for further details).

calcite precipitated from seawater. Modelling Mg content of inorganic calcite over a larger range of Mg/Ca (i.e. including the freshwater realm) might help to distinguish if the temperature dependence of Mg/Ca observed for ostracods is due to inorganic processes or if biological processes have to be involved.

An increase of 3 % in Mg/Ca ratio per °C (Lea, 2003), if correct, has several important implications. Theoretical relationships between Mg/Ca ratios of hypothetical ostracod taxa having different affinities for magnesium at different water temperatures are modelled in Figure 1.6. The model shows two

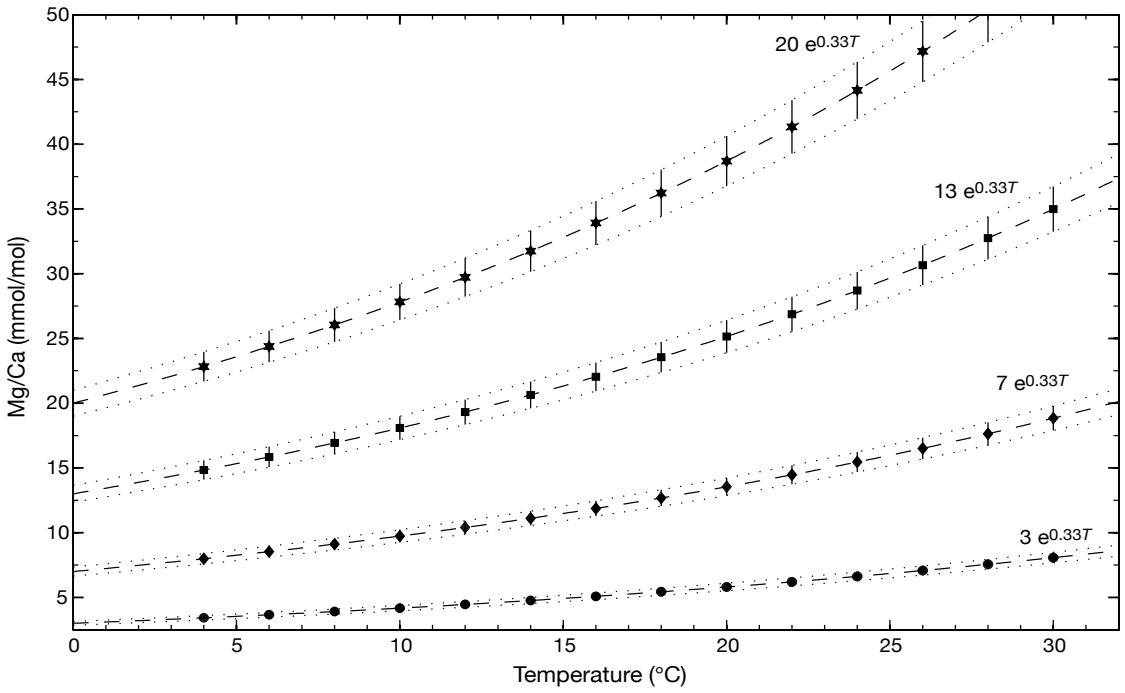


FIGURE 1.6
Model illustrating an exponential increase of 3.3 % in Mg/Ca ratio of ostracod shell per 1°C for different initial concentration of magnesium (3, 7, 13, and 20 mmol/mol Mg/Ca). Vertical bars and dashed lines represent an anallytical error of 5 %.

important facts. The first one is that the sensitivity for temperature changes is higher in species having high Mg/Ca. The second one is that sensitivity for temperature changes is higher at high temperature than in fresh conditions. These two particularities were already postulated by De Deckker and co-authors (1999) on the basis of data obtained from laboratory cultures.

Beside these general considerations, laboratory and natural environmental studies showed that in most of the cases, the incorporation of magnesium in ostracod valves is dependent on the Mg/Ca of water as well as water temperature (Chivas, et al., 1983, 1986; Engstrom and Nelson, 1991; Dwyer et al., 1995; De Deckker et al., 1999, Palacios-Fest and Dettman, 2001; Cronin et al., 2005; Kondo et al., 2005). In some natural system, Mg/Ca ratio of water and water temperature vary concomitantly. In these conditions, it can be very difficult to separate the effect of water temperature from the effect of increasing water Mg/Ca ratios (Wansard and Mezquita, 2001; Dettman et al., 2002)

2.3.4. Strontium partitioning

Incorporation of strontium into inorganic and biogenic calcite precipitated from seawater has been well-studied during the last 30 years. Strontium content in calcite is mainly controlled by two parameters: growth rate and temperature. In general, strontium incorporation into both inorganic and organic calcite increases with increasing calcification and precipitation rate, respectively (see Tang et al., 2008). The effect of temperature, on the other hand is more controversial. Tang and co-authors noted in 2008: "for inorganic calcite spontaneously precipitated from a strontium-bearing solution a negative temperature dependence of strontium is obtained, whereas for biogenic calcite and experimental transformation of aragonite and dolomite to inorganic calcite, a positive or insignificant temperature dependence was observed". Beside, Mucci and Morse (1983) observed that in calcite precipitated from seawater (i.e., containing both Mg and Sr), the Sr incorporation was linearly related to the Mg content of the mineral, which they attributed to an increase in the solubility of $SrCO_3$ in calcite due to the incorporation of the smaller Mg^{2+} ions.

Ostracods grown in the laboratory and collected in natural environments allow us to observe which parameters control incorporation of strontium. In Loxoconcha matagordensis, strontium content increases linearly with shell weight (Dwyer et al., 2002). The latter is believed to reflect the completeness of shell secretion. Thus, the relative depletion in Sr of non-complete calcified valves indicates that the Sr is incorporated into the calcite during the last stage of valve calcification. Almost all the studies investigating strontium uptake show that the major parameter controlling strontium content in ostracod

valve is the Sr/Ca ratio of host water (Chivas et al., 1983, 1986; De Deckker et al., 1999; Engstrom and Nelson, 1991). Among the different studies, some observed no temperature dependence for strontium uptake (Engstrom and Nelson, 1991) or only a slight dependence (Chivas et al, 1983, 1986; Dwyer et al., 2002). De Deckker and co-authors proposed in 1999 that at low temperature, the incorporation of strontium was temperature dependent whereas it is temperature independent at higher temperatures. The last study to date on ostracod in a dilute freshwater system presented a high correlation between strontium and magnesium content in the valve of Herpetocypris intermedia (Wansard and Mezquita, 2001). The authors of this study associated the variation of strontium in the shells to the variation of Sr/Ca ratio in water. Dettman and co-authors (2002), on the basis of the same dataset, conclude that the major control on strontium content in the shell was the water temperature. The disagreement between both interpretations ensues from the concomitant variation of both Sr/Ca ratio of water and temperature.

3. Aims and Design of the Study

As stated above, the principal aim of the present study is to establish how the environmental parameters are recorded in ostracod valves. In other words, the goal is to 'calibrate' the use of ostracod valve geochemistry as a proxy. The stable isotope fractionation factors (carbon and oxygen) and trace element (magnesium and strontium) partitioning coefficients have to be determined for the different species inhabiting Lake Geneva. In addition, the factors controlling water chemistry (Mg/Ca and Sr/Ca ratios) and isotopic composition ($\delta^{18}O_{H2O}$ and $\delta^{13}C_{DIC}$) must be well-defined in order to understand which phenomenona are actually recorded in ostracod valves.

To achieve this, a natural 'culture' environment approach was adopted. The preference of natural environment experiment over laboratory cultures is justified by several reasons. First of all, fossil ostracods grew in a natural system; thus, the natural environment approach is the "experiment" in which the conditions are closest to what the ostracods experienced before being incorporated into the sediment as fossils. Secondly, laboratory cultures often results in stressful conditions for the ostracods, leading to non-complete valve calcification and potential geochemical biases (Engstrom and Nelson, 1991; Xia et al, 1997). In natural environments, these problems are avoided because the animal occurs only when its ecological demands are fulfilled. If the specific species is not adapted to prevailing external conditions, the species inevitably fade out and is eventually rapidly replaced by another more competitive one. In other words, equilibrium is the rule in natural systems. Thirdly, the animal can be observed in its natural environment and crucial information about its autoecology can be obtained. Finally, the lake provides a natural, huge aquarium in which living ostracod can simply be collected, while the seasonality provides major environmental changes through the years. Hence, five sites from 2 to 70 m water depths (2, 5, 13, 33, and 70 m) were selected in Lake Geneva to sample living ostracods and monitor environmental parameters.

Two types of data are necessary to determine how isotopes are fractionated and trace elements partitioned during valve calcification: environmental parameters and geochemical composition of ostracods. Naturally, the environmental parameters must correspond to the conditions experienced by the animal as it calcified its shell. Ostracods were, therefore, collected alive during a one-year cycle at one-month intervals. Environmental parameters were monitored in parallel as continuously as possible.

In this study, two types of environments were investigated: bottom water and interstitial water. Bottom water, corresponds to the water lying just above the sediment. Interstitial water corresponds to the water contained in the top centimetres of sediment. Environmental parameters include water temperature, pH, dissolved inorganic carbon concentration ([DIC]) and its carbon isotope composition ($\delta^{13}C_{DIC}$), oxygen isotope composition of water ($\delta^{18}O_{H2O}$), and calcium, magnesium, and strontium concentration of water (Mg/Ca_{H2O} and Sr/Ca_{H2O}).

Biological and autoecological observations include ontogenesis, life-cycle, male to female ratio, population density, bathymetric distribution, macro- and micro-habitat preferences, sediment penetration depths, valve weight, and valve morphometry.

Geochemical composition of ostracod valves embraces carbon and oxygen isotope composition ($\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$) and magnesium and strontium content (Mg/Ca_{ostra} and Sr/Ca_{ostra}).

The above dataset will then be interpreted in terms of the species autoecology and the environmental conditions at the time of valve calcification. This approach necessitates sound knowledge on the ostracod species-specific autoecology and on the spatial and temporal variation of environmental

parameters. Hence, this project focuses on these two major aspects.

4. Thesis Outline

The present thesis consists of six main chapters and appendixes. The base of the text is composed of five manuscripts written to be submitted to international peer-reviewed journals. To give the thesis a guiding thread, the different manuscripts were regrouped according their specific theme. To avoid repetition, similar part of text were displaced or removed.

A general introduction and theoretical background were given in Chapter I. The aim and the design of the study as well as the state of the art on ostracod biomineralisation and geochemistry form the main part of this chapter.

Chapter II focuses on the geographical setting and methods. This chapter actually regroups geographical settings and method sections of the different manuscripts. General geographical, geomorphologic and limnological information on Lake Geneva is given. Sampling sites are described. The methods used to monitor the different environmental parameters as well as to sample water are detailed for both open and interstitial water. Sampling, separation, and the preparation of ostracods for further analyses are described. Analytical procedures for sediments, water samples, and ostracod valves complete this second chapter.

In Chapter III, the autoecology of ostracods is discussed. This chapter is divided into two sub-chapters, each one written as manuscripts ready for submission or already submitted for publication. The aim is to publish the two manuscripts of chapter III as companion papers in *Hydrobiologia*, an international peer-reviewed journal investigating the biology of all aquatic environments. The first sub-chapter illustrates the use of a new method to represent ostracod life-cycles in a synthetic manner. As an example, the life-cycle of *Candona neglecta*, a dominant species of Lake Geneva particularly interesting for palaeoclimatic research, is analysed. The second sub-chapter presents the autoecology, mainly the population density, the species life cycle and macro- and micro-habit preferences of the different species encountered alive in Lake Geneva. The influence of the major environmental parameters on ostracod population (temperature, oxygen content, and substrate type) is discussed in the light of the modern dataset and the evolution of fossil assemblages separated from a sedimentary short core taken in the profundal zone of the “Petit-Lac” (western basin of Lake Geneva).

Chapter IV describes the spatial and temporal variation of environmental parameters. When possible, the different mechanisms controlling these variations are explained. The focus of this manuscript was not only to discuss environmental conditions but rather to examine how these interact with ostracods and how they might influence valve geochemistry. Biomineralisation processes and non-equilibrium incorporation of trace elements and stable isotopes are not taken into account at this stage of the discussion. This chapter consists of a manuscript to be submitted to a journal specialised in geochemistry or in palaeoenvironmental research such as *Geochimica et Cosmochimica Acta*, *Chemical Geology*, or *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Chapter V focuses on ostracod valves geochemistry. This chapter regroups two manuscripts to be submitted as companion papers in *Geochimica et Cosmochimica Acta*. The first sub-chapter examines the carbon and oxygen isotope fractionation during ostracod valve calcification. Potential mechanisms leading to isotopic disequilibrium are discussed thoroughly. The second sub-chapter deals with magnesium and strontium uptake in ostracods. Valve geochemistry is examined in details and compared to environmental parameters. As partition coefficients are known to vary greatly from site to site, the relationship between the different parameters are compared rather than the values themselves. To get a grasp of which parameters control ostracod trace element contents, the theoretical responses of ostracod shells to different types of controls were established and compared to the present dataset as well as data issued from the existent literature.

Chapter VI synthesises the preceding chapters. The potential of ostracod fossils as palaeoenvironmental proxy in Lake Geneva are generally discussed. Finally, future prospects are given at the end of the thesis.

The following appendix is divided in two parts. The first one illustrates graphically the results for each species. The amount of data being too considerable to be placed in the discussion without disturbing its clarity, it was decided to place them in the appendixes. Hence, only the syntheses are illustrated in the main text. This unfortunately may “hide” some detail of the work since the raw data was treated prior presenting the final results. It is, therefore, important that all the data are published so that interested or sceptical

readers can verify data treatment and interpretations. Monthly and relative ostracod abundances, life-cycles, sediment penetration depths, oxygen isotope fractionation factors, carbon isotopic compositions and relationships between environmental factors and magnesium and strontium contents are illustrated for each species in Appendix I.

Appendix II is a more classical appendix with all results obtained during the study presented as numerical tables.

Chapter II :

GEOGRAPHICAL SETTINGS AND METHODS

1. Study Site

Lake Geneva is the largest freshwater lake in Western Europe with a surface area of about 580 km^2, a total volume of 89 km^3 and an outflow of 250 m^3/s. Its basin occurs within the Molasse sedimentary rocks of the Alpine foreland, between Switzerland and France (Fig. 2.1 A). It is divided into two contrasting sub-basins: the "Grand-Lac" (eastern part) and the "Petit-Lac" (western part). Differences between these two basins are not only morphological but also physico-chemical.

The "Grand-Lac" is a large, deep basin with a maximum depth of 310 m and a mean depth of 172 m. Because of its large depth and relatively mild winter temperature, this main basin is generally meromictic, where only the first 100 meters of water mixes during winter and is monomictic only during very cold winters. Deeper waters are only regenerated on average every 3 to 4 years (e.g., CIPEL, 1984). In contrast, the "Petit-Lac" is a medium-sized basin, 23.3 km long, 4.7 km wide, having a mean water depth of 41 m and a maximum depth of 76 m. This basin accounts for only 4 percent of the total volume of water of the entire lake. It is monomictic and deep water is well oxygenated throughout the year because of the annual overturn in winter and the mixing induced by wind.

As it is the case for other lakes in Europe, Lake Geneva was influenced by an anthropogenic overload of nutrients during the 20th century. The increase in productivity, in parallel with warmer winter periods, leads to oxygen depletion in the deep water of the "Grand-Lac". These phenomena have, to a lesser extent, also affected the "Petit-Lac".

The "Petit-Lac" is a mesotrophic, soft water lacustrine system with a pH of approximately 8. It is sulphate dominated (about 46.5 mg/l $SO_4^{2-}$and 8.7 mg/l Cl^-) with a relatively low salt content (Ca^{2+}: 42 mg/l, Na^+: 5.9 mg/l, Mg^{2+}: 5.5 mg/l, K^+: 1.31 mg/l) and a total alkalinity of 1.7 meq/l. Water temperature varies between 4.4°C and 26.6 °C and oxygen concentration

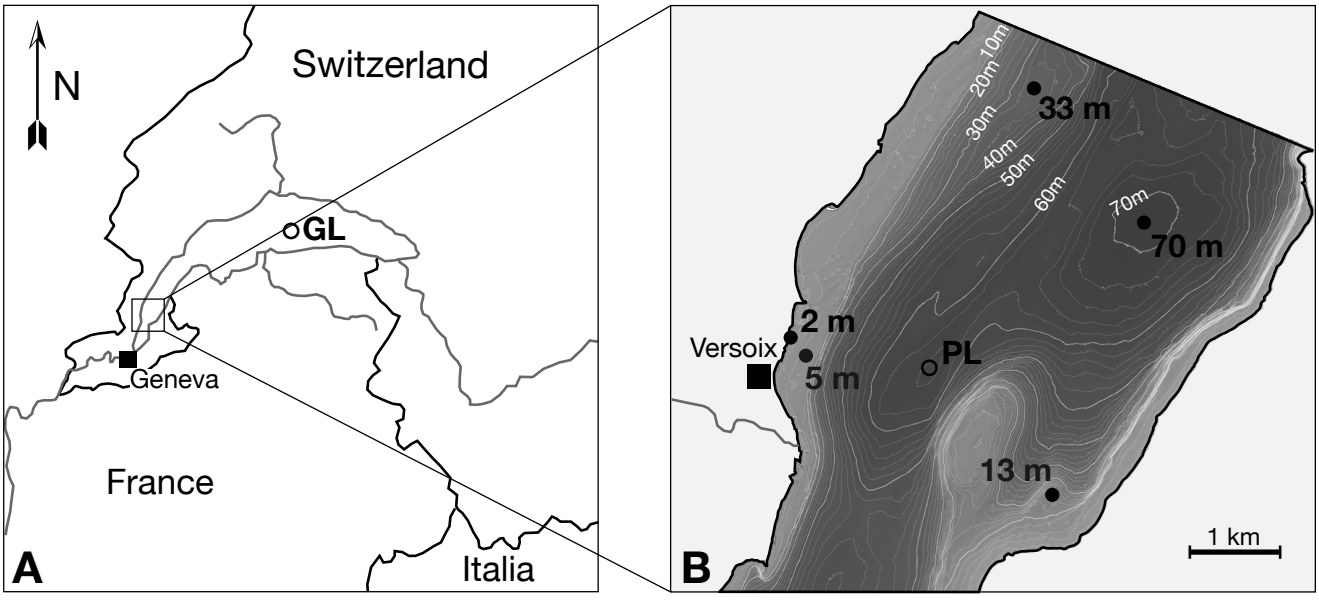


FIGURE 2.1
Geographical setting of Lake Geneva, Switzerland (A) and the five sampling sites at 2, 5, 13, 33, and 70 meters water depths in the «Petit-Lac» (B). Unfilled circles GL and PL are the emplacement of column water profiles sampled in the "Grand-Lac" and the "Petit-Lac", respectively. Bathymetric map modified from «Bathymétrie du Petit-Lac Genevois, Lac Léman» from Institute Forel, University of Geneva.

ranges from 7.9 mg/l to 14.7 mg/l from April 2006 to May 2007 ("service de l'écologie de l'eau" SECOE, pers. com.).

Because of its good oxygen supply, relatively quiet autochthonous dominated sedimentation and geomorphologic characteristics, the "Petit-Lac" was chosen for this study. Five sampling sites situated along gently sloping declines have been chosen at different water depths (2, 5, 13, 33, and 70 m; Fig. 2.1 B).

TABLE 2.1
Sampling schedule.

Sampling sites	13 and 70 m		2, 5, and 33 m	
Sampling sessions and dates	A	04.07.06	A	04.07.06
	B	04.19.06	C	04.25.06
	D	05.10.06	E	05.24.06
	F	06.12.06	G	06.19.06
	H	07.11.06	I	07.25.06
	J	08.10.06	K	08.31.06
	L	09.12.06	M	10.04.06
	N	10.10.06	O	10.25.06
	P	11.15.06	Q	11.28.06
	R	12.12.06	S	01.09.07
	T	01.16.07	U	02.15/16.07
	V	02.20.07	W	03.12.07
	X	03.27.07	Y	04.10.07
	Z	04.25.07	aa	05.01.07

2. Field work

2.1. Schedule of the Sampling Sessions

Table 2.1 presents the planning of the different sampling sessions. Each station was visited once per month during a one-year cycle from April 2006 to May 2007. Because a single day was too short to investigate the five sites and because ostracods needed to be separated alive and as rapidly as possible, only half of the sites were visited at a time. The remaining ones were visited approximately a half-month later. Thus, at the start of the studied period, sites at 13 and 70 m water depths were visited at the beginning of the month, whereas sites at 2, 5, and 33 m water depths were visited in the middle of the month. This scheme was rapidly modified because of unfavourable meteorological conditions (see Table 2.1).

2.2. Physical and Chemical Parameter Monitoring

At the two shallower sites (2 and 5 m water depths), pH, water temperature, and oxygen concentration were measured in situ with a probe. In the deeper sites (13, 33, and 70 m water depths), pH, water temperature, and oxygen concentration were directly measured in sedimentary short cores just above the water-sediment interface. To reduce contact with the atmosphere and warming of water, a new core was used for each manipulation. Periodically, pH of the interstitial water was measured every 0.5 cm along sediment depth profiles using a "WPI Beetrode" micro pH electrode (NMPH2) and a "Dri-ref" reference electrode (DRIREF-2). pH profiles were only obtained where short cores could be retrieved, i.e. at 13, 33, and 70 m water depths.

In addition, water temperature was measured continuously every three hours from January 2006 to July 2007 with data-loggers (Vemco Minilog) installed at the four shallower sites (2, 5, 13, and 33 m water depths). Water temperature was also measured in situ in all sites with a probe on a monthly basis. Water temperature at 70 m from 23.01.06 to 20.03.06 and on 21.05.07 were measured by the "service de l'écologie de l'eau" (SECOE) of the state of Geneva (SECOE, pers. com.)

2.3. Water Sampling

2.3.1. Bottom water

At the two shallower sites (2 and 5 m water depths), the substratum consists of pebbles, sandy beds and algae. Bottom water was collected using a "go-flow water probe" system. In contrast, sediments at the three deepest sites (13, 33, and 70 m water depths) consist of silty-sand and clayed-silt. At these sites, a short gravity corer was used to recover sediment and supernatant water. Water lying over the water-sediment interface was sampled using 50 ml syringes. Directly after being collected, water was filtered with 0.20 µm 'Nalgene' filters and stored in 30 ml brown glass bottles. All water samples were kept in a cold box for transport to the laboratory of the University of Lausanne, where they were kept refrigerated until processing. Water samples for elemental analyses were acidified afterward in the laboratory to 5% with Merck Suprapur HNO_3. To assess contamination, blanks were periodically prepared directly on board using Milli-Q water (18 Ωm).

2.3.2. Interstitial pore water

The geochemistry of interstitial water was studied using short sediment cores retrieved once per

season at 13, 33, and 70 m water depths. Slices of one centimetre along the top five centimetres were directly sampled on board using a piston device. Each slice of fresh sediment was then rapidly wrapped in a nylon mesh of 45 µm and the whole introduced in a 50 ml syringe. The air contained in the syringe was immediately evacuated. One 'Nalgene' pre-filter of 1 µm coupled with one 'Nalgene' filter of 0.2 µm were directly mounted in line on the syringe. Interstitial pore water contained in the sediment was sampled by applying pressure on the piston. Using this method, about 3 to 15 ml of water could be extracted from each sediment slice. Water samples for carbon isotope measurement of the dissolved inorganic carbon ($\delta^{13}C_{DIC}$) were stored in 3 ml glass vials; the rest of the water was poured in "Semadeni" 10 ml polypropylene vials and acidified afterward in the laboratory to 5% with Merck Suprapur HNO_3 for elemental analyses. The squeezed sediments were recovered after water extraction and dried during one night in an oven at 40°C for subsequent geochemical analyses. To assess contamination, blanks were prepared on board using the same method but with MilliQ water (18 Ωm) instead of lake sediment.

Using this extraction method may lead to significant gas exchange between atmosphere and interstitial water. In addition to change in the concentration of dissolved inorganic carbon ([DIC]), this may affect the carbon isotope composition of dissolved inorganic carbon ($\delta^{13}C_{DIC}$). Beside, this may also change the redox potential in the sediment sample and this would affect the interstitial water elemental composition. To minimize these undesirable effects, all manipulations were made as rapidly as possible to reduce the exposure time of the sediment as much as possible. The conventional method requires sampling of the sediment and water under an anaerobic atmosphere, typically in a glove box filled with nitrogen. Moreover, extraction of interstitial water is commonly done by centrifugation. This method was not applied here for the following reasons. Firstly, as bottom water is well oxygenated in the "Petit-Lac", superficial sediment is not reduced and only the deepest sediments may be reductive. A slight contact with the atmosphere is, therefore, less dramatic than for anoxic conditions. Secondly, sampling was done using a moderately-sized vessel; it was therefore not possible to install a glove box on board. Thirdly, to avoid disturbing the sediment and temperature change during transport to the laboratory, rapidity was preferred over anaerobic sampling in the laboratory. Finally, sampling sessions were initially planned to recover living ostracods. Extraction of interstitial water was, therefore, only done when extra time was available.

2.4. Living Ostracod Samples

At 13, 33, and 70 m water depths, undisturbed fresh sediments recovered with the help of a short gravity-corer were used to collect living ostracods. To investigate ostracod penetration depth, slices of fresh sediment of 0.5 cm down to 2 cm and of 1 cm down to 5 cm were sampled directly on board using a piston device. While meteorological conditions were calm, 4 to 5 cores were taken, otherwise only 2 to 3 cores. At 2 and 5 m, a sediment grab was used to recover pebbles, sand, and algae. Sediments of all sites were placed in flasks closed with a pierced lid, stored during transport to the laboratory of the University of Lausanne in a cold box and kept refrigerated until further processing.

3. Ostracod Separation and Treatment

3.1. Ostracod Separation

To accelerate and facilitate ostracod separation, samples were washed in a 200 µm mesh sieve. Residues were transferred with tap water into Petri dishes. Living ostracods were taken up using Pasteur pipettes under a stereomicroscope and killed in 30% alcohol. The animals were then stored in pure ethanol. All samples were processed during 24 to 48 hours, rarely 72 hours, following sampling.

3.2. Taxonomy, Ontogenesis, and Specimen Abundance

For species identification, micro-dissections of soft parts were often carried out on male and female adults and on juvenile stages A-1 to A-3, following the method of Danielopol (1982). Identification and taxonomy are based on Meisch (2000), Danielopol (1969) and Absolon (1978). Identification of adult and juvenile stages is based on appendage development (Danielopol and Tetart, 1990; Henderson, 1990) and valve size. Abundance of adults and juveniles of A-4 to A-1 instars were determined; gender was established for adults and A-1 instars ('A-X instars' denotes the specimens that belong to development stage A-X, see Meisch, 2000 for general information on ostracod development). The abundance of each instar was expressed as monthly mean abundance per core (1

core = 26.4 cm^2). The 'monthly total population' is equal to the sum of individual abundances of adults and juvenile stages A-1 to A-4 for each month. The 'monthly relative abundance' equals the 'monthly individual abundance' of each instar divided by the 'monthly total population' and is expressed in percent. 'Mean annual population density' equals the average of the 'monthly total population' normalized for 1 m^2; 'maximum population density' is the highest 'monthly total population' normalized for 1 m^2. 'Annual productivity' is the sum of all females recovered during the year normalized for one core; 'net productivity' is the average of females per productive month (i.e., months during which adult females are present) normalized for one core. Life histories are displayed using a newly developed Synoptic Ostracod Watch Model (SOWM; see Sub-Chapter 3.1).

3.3. Sediment Penetration Depth

To analyse ostracod penetration depth, only data from cores with undisturbed sediments that were sub-sampled rapidly have been used. Instar abundances were normalised for 0.5 cm of sediment, i.e. values for slices of 1 cm thickness were divided by 2. Relative percentages of specimens of each instar per sediment interval to total specimen abundance of the specific instar were calculated. The distribution of A-4 specimens was identical to the distribution of A-3 specimens; therefore, only results for stage A-3 to adult are illustrated.

3.4. Treatment for Geochemical Analyses

Dead animals were kept in a 4 % NaOH solution during 4 hours to remove soft parts. Empty and disarticulated valves were thereafter thoroughly rinsed step by step with tap water, distilled water, and ethanol (Merck absolute G.R for analyses), and finally permitted to dry at room temperature (for ostracod pre-treatment methods, see Danielopol et al., 2002; Keatings et al. 2006; and Mischke et al., 2008b). All valves were then separated according to species, gender, and instars and weighted separately (in general adults and A-1 instars) or by batches (small forms and A-2 instars). For analyses, valves were recombined to reach acceptable sample size (≥ 50 µg when possible). Valves of different development stages were not mixed and valves of different gender were in general analysed separately. For dates with a very low number of specimens, valves of two different sampling sessions, but issued from the same sampling site, could be combined but care was taken in order that the environmental conditions experienced by the animals were analogous. All samples were then manually washed under a stereomicroscope with a 000 paint brush in Milli-Q water (18 Ωm) to remove any impurities and rinsed with pure ethanol before being placed in the borosilicate vials dedicated for isotopic analyses. These last manipulations were carried out in the clean lab to avoid dust contamination, especially for the trace element analyses.

4. Analytic Procedures

4.1. Sediment Samples

Carbon and oxygen isotope composition of carbonates ($\delta^{13}C_{CaCO3}$ and $\delta^{18}O_{CaCO3}$) were measured on bulk sediments treated three times during 24 hours with 4% NaOCl to remove organic matter. Isotopic composition was determined using a standard acidification method at 70°C (Spötl and Vennemann, 2003) with a Gasbench II coupled to a ThermoFinnigan^{plus}XL isotope ratio mass spectrometer (IRMS) at the Stable Isotope Laboratory of the University of Lausanne. For standardisation, an internal laboratory standard (Carrara Marble) calibrated to VPDB was used. Analytical precision was better than ± 0.1 ‰ for $\delta^{13}C_{CaCO3}$ and ± 0.2 ‰ for $\delta^{18}O_{CaCO3}$. If standard weights are measured prior to isotopic analyses, it is possible to estimate the carbonate content of the sample using a simple regression method. The sediment carbonate content (% $CaCO_3$) is calculated using a regression lines obtained from first peak intensities (m/z = 44/45/47) versus standards weights and first peak intensities of the measured samples. Uncertainty for % $CaCO_3$ is estimated to be approximately 5%.

To determine the carbon isotopic composition of bulk organic matter ($\delta^{13}C_{OM}$), samples were acidified three times during 24 hours with 30% HCl to remove carbonates and analysed with a Carlo Erba 1108 elemental analyser (EA) connected to a Finnigan MAT Delta S isotope ratio mass spectrometer (IRMS) via a Conflo II split interface (EA/IRMS) at the Stable Isotope Laboratory of the University of Lausanne. Three internal laboratory standards calibrated to VPDB were used to assess the $\delta^{13}C_{OM}$ values. Percentage of total organic carbon (%, TOC) was estimated using the regression method described above. Analytical precision for $\delta^{13}C_{DIC}$ was better than ± 0.2 ‰ and estimated at ± 5% for TOC. Percentage

of total nitrogen content (%, N) was measured using same regression method but without establishing the isotopic composition. Analytical precision for amount of nitrogen is estimated at ± 5%. Oxygen and carbon isotope composition of carbonate and organic matter are always reported in the δ-notation relative to VPDB (Vienna Peedee Belemnites) following the expression:

$$\delta X = ((R_{sample}/R_{standard})-1) +1000 \qquad (2.1)$$

where δX is the delta value of the sample for element X (H, O, C, etc.) in parts per thousand ("per mil," ‰) and R is the molar ratio of the heavy (less common) to light (more common) isotope in the sample and in an international standard, respectively.

4.2. Water Samples

Dissolved inorganic carbon concentration ([DIC]), carbon isotope composition of dissolved inorganic carbon ($\delta^{13}C_{DIC}$), and oxygen isotope composition of water ($\delta^{18}O_{H2O}$) were determined with a Gasbench II coupled to a ThermoFinnigan^{plus}XL isotope ration mass spectrometer (IRMS) at the Stable Isotope Laboratory of the University of Lausanne.

Determination of DIC concentrations and $\delta^{13}C_{DIC}$ values were made not later than 3 to 4 weeks after sampling, following a modified method after Spötl (2005). For standardisation, an internal laboratory standard (Carrara Marble, $\delta^{13}C$ = 2.05 ‰ VPDB, $\delta^{18}O$ = –1.70 ‰ VPDB) calibrated to VPDB was used. Analytical precision for $\delta^{13}C_{DIC}$ was better than ± 0.2 ‰. DIC concentrations were estimated using the regression method described above using first peak intensities versus Carrara Marble standard weights. [DIC] is expressed in mmol/kg and analytical precision is estimated to be approximately ± 5%.

For determination of the oxygen isotopic composition of water ($\delta^{18}O_{H2O}$), samples were equilibrated with CO_2 for 24 hours and the latter analysed following a modified method after Seth and co-authors (2006). To assess $\delta^{18}O_{H2O}$ values, three internal laboratory standards calibrated to VSMOW were used ($\delta^{18}O_{INH}$ = –17.00 ‰ VSMOW, $\delta^{18}O_{MOW}$ = 0.39 ‰ VSMOW, $\delta^{18}O_{LIPE}$ = –8.50 ‰ VSMOW). Analytical precision for $\delta^{18}O_{H2O}$ was better than ± 0.15 ‰.

Concentrations of magnesium, calcium, and strontium (Ca^{2+}, Mg^{2+}, and Sr^{2+}) in water were measured with an APEX connected to a Perkin-Elmer ELAN 6100 DRC induced coupled plasma mass spectrometer (ICP-MS) at the Institute of Mineralogy and Geochemistry of the University of Lausanne. Water samples were diluted 10 times in Milli-Q water (18 Ωm) and acidified to 5 % with Merck Suprapur HNO_3. Single Elemental Standards for ICP-MS analyse ('Analab') were used for internal and external standardisation. Two external standard solutions were prepared with different concentrations of calcium, magnesium and strontium. Rhodium was added in all samples, blanks, and standards for internal standardization. During the analyses, detection limits depended of the quality of the different blanks prepared in the field and varies slightly from one analyses sequence to the other. Intensity measured on the different masses for water samples were at least 40 times higher than for blanks. Routine analytic reproducibility of the laboratory for this type of analyses is approximately ± 5%. Results are express as Mg/Ca and Sr/Ca molar ratios.

Calcite saturation index was calculated using values of [DIC], pH, Ca^{2+} concentration, and temperature using PHREEQC program.

4.3. Ostracod Shells

Carbon and oxygen isotope composition of ostracod shells and standards were determined with a Gasbench II coupled to a ThermoFinnigan^{plus}XL isotope ration mass spectrometer (IRMS) at the Stable Isotope Laboratory of the University of Lausanne following standard method of acid digestion at 70°C (Spötl and Vennemann, 2003). Because subsequent trace element analyses were planned, acidification was done using Merck Suprapur orthophosphoric acid having originally 65 % weight of acid. Water of this acid was previously extracted using a vacuum line. The orthophosphoric acid was placed in a silicate glass (SiO_2–pure glass), which was gently warmed up at the same time that air and water were pumped out using a vacuum line of the laboratory. To assess the distillation of the acid, the acid weight percent was periodically determined using a gravimetrical method (Burman et al., 2005). The final acid had a percent that reached approximately 96 wt%. For isotopic analyses, an internal laboratory standard (Carrara Marble) calibrated to VPDB was used normalize the final δ–values. For small samples (in general < 70 µg), values had to be corrected as a function of the sample weight (estimated with 1st peak area for m/z = 44, 45, and 47) following the method suggested by Spötl and Vennemann (2003). Figure 2.2 shows the $\delta^{18}O$ and $\delta^{13}C$ values of all standards, corrected when necessary for sample size, used during the analysis period. The precision decreases with decreasing

sample size but accuracy is preserved over the whole sample size range. For large samples, the long-term uncertainty (1-sigma) is 0.06 ‰ for carbon and 0.07 ‰ for oxygen. Uncertainty increases to 0.19 ‰ for carbon and 0.16 ‰ for oxygen for the smallest samples (approximately 20 to 30 µg).

Once isotopic analyses were completed, vials containing the acid residue were recovered and brought to the clean lab. There, acid residues were diluted in 10 ml Milli-Q water (18 Ωm) and transferred in 10 ml 'Semadeni' polypropylene vials and kept refrigerate until further analyses.

Concentrations of magnesium, calcium, and strontium (Ca^{2+}, Mg^{2+}, and Sr^{2+}) were measured with an APEX connected to a Perkin-Elmer ELAN 6100 DRC induced coupled plasma mass spectrometer (ICP-MS) at the Institute of Mineralogy and Geochemistry of the University of Lausanne. Before analyses, samples were acidified to 4% with 65% Merck Suprapur HNO_3. Single Elemental Standards for ICP-MS analyses ('Analab') where used for internal and external standardisation. Two external standard solutions were prepared with different concentrations of calcium, magnesium and strontium to recalculate sample elemental concentrations. Indium and Scandium were added to samples, standards and blanks (0.05 ppm) for internal standardisation. Calcium and magnesium intensities were calibrated using scandium intensities whereas indium intensities were used for strontium. During each isotopic run, one blank, i.e. an empty vial, was placed in the batch. These blanks experienced exactly the same sample handling procedures and permitted us to assess contamination due to traces within the H_3PO_4 acid used for isotopic analyses and/or due to the release of elements from the borosilicate glass vessels in contact with 96% H_3PO_4 acid at 70 °C during the 24 hours required for the isotopic measurement. Elemental analyses indicated that blanks were significantly enriched in magnesium and calcium but only slightly in strontium. Therefore, samples and blanks issued from the same isotopic run were analysed in the same ICP-MS run and measured sample intensities were corrected with the intensities measured for the respective blanks. For small samples, i.e. samples with low amounts of calcite, magnesium and sometimes calcium intensities measured were equivalent or only slightly superior to the intensities measured on the blank. Hence, to prevent as much as possible any errors due to the variation of contamination within a single batch, sample intensities lower than three times blank intensities were discarded. This operation excluded a large amount of data of magnesium but excluded only few data of calcium and strontium

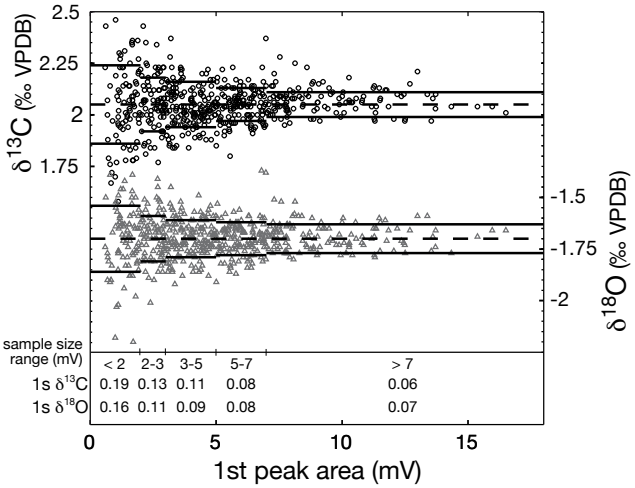


FIGURE 2.2
Stable isotope compositions of carbon (black dots) and oxygen (grey triangle) of the internal standard (Carrara Marble) corrected for sample size and calibrated relative to VPDB used to recalculated delta values of ostracod samples. Dashed lines represent NBS value of 2.05 ‰ for carbon and -1.70 ‰ for oxygen, solid lines represent the 1-sigma standard deviation for different sample size ranges. Note the decrease of the precision with decreasing sample size, whereas accuracy remains stable over whole sample size range.

because contamination for these two elements was less problematic. Results are expressed as Mg/Ca and Sr/Ca mole ratios. Routine analytic reproducibility of the laboratory for this type of analyses is approximately ± 5%. Trace element contents of ostracod shells are expressed as Mg/Ca and Sr/Ca molar ratios.

Chapter III - 1 :

RECENT OSTRACODS IN LAKE GENEVA (SWITZERLAND): PART I. DETAILED STUDY OF THE LIFE-CYCLE OF *CANDONA NEGLECTA* SARS, 1887 (CRUSTACEA, OSTRACODA, CANDONIDAE)

1. Introduction

Ostracods are sensitive to ecological parameters and can be used as potential bio-indicators (Külköylüoğlu, 2004). Given that their low-magnesium calcite carapace is also well preserved in lake and ocean sediments, these small crustaceans are hence also very useful for palaeoenvironmental interpretations. Presence or absence of certain species, and quantitative population analyses of living or fossil assemblages permits an estimation of many ecological characteristics of their habitat (Carbonel et al., 1988; Mezquita et al., 2005; Viehberg, 2006, Dügel et al., 2008). In addition, morphometry and geochemistry of their shells can be used to reconstruct similar variables in an often quantitative fashion (Holmes and Chivas, 2002; Cronin et al., 2005; Keatings et al, 2007). The main parameters influencing ostracods are the chemical composition and temperature of the water as well as its flow velocity (Roca and Baltanás, 1993; Mezquita et al., 1999b; Smith and Horne, 2002; Horne, 2007). The importance of these parameters on the development of the ostracods depends of the type of aquatic habitat. For example, the chemical composition of water is variable in estuary or closed basins in arid regions. In contrast, water temperature is the main fluctuating parameter in open, permanent water bodies because their chemical composition varies only slightly and/or is often directly or indirectly affected by variation of the water temperature itself. These parameters can vary seasonally or on a longer time scale. As ostracods grow by moulting and not by continuous accretion of calcite, they are not only affected by the long term variations of the environmental parameters but much more by the particular environmental parameters that prevail just during the formation of its carapace. As seasonal variations of these parameters are generally larger than long-term variations, precise knowledge of timing of moulting, and thus of their specific life history, is essential for palaeoenvironmental reconstructions based on ostracod fossils.

Importance of the type of habitats on the life history of freshwater ostracods was already postulated at the beginning of the 20th century for freshwater ostracods of Central and Northern Europe. Alm (1915) described life cycles in different environments in Sweden and suggested that life history of these organisms is linked to the type of environment where they grow. Wolf corroborated these observations in 1920 in the region of Basel in northern Switzerland. Hiller, in 1972, studied the biology and ecology of the freshwater ostracods in the neighbourhood of Hamburg and observed also different development types according to different environments. These observations were also carried out in brackish water environments by Savolainen and Valtonen in the Baltic Sea in 1983. Many other studies have described the life cycle of ostracods at various detail levels. Nevertheless, for certain species no or only very little information exists and descriptions of the life cycles are not well known. This is also the case for the life cycle of certain well-known species in environments with difficult access such as the deepest zone of lake basins. There are also some discrepancies between different studies that are still not explained. This is the case, for example, for *Candona neglecta*, a very common and wide spread species that is often used in palaeoenvironmental studies and has different life cycles.

Here, we present the life cycle of *Candona neglecta* (Sars, 1887) at different depths in modern Lake Geneva, Switzerland. To facilitate the interpretation, we use a novel approach to depict qualitatively the life-cycle of ostracods permitting to recognize the main features at a glance. This method is used to compare our dataset with previous results and discuss the development of *Candona neglecta* as well as other biological features under different environmental conditions.

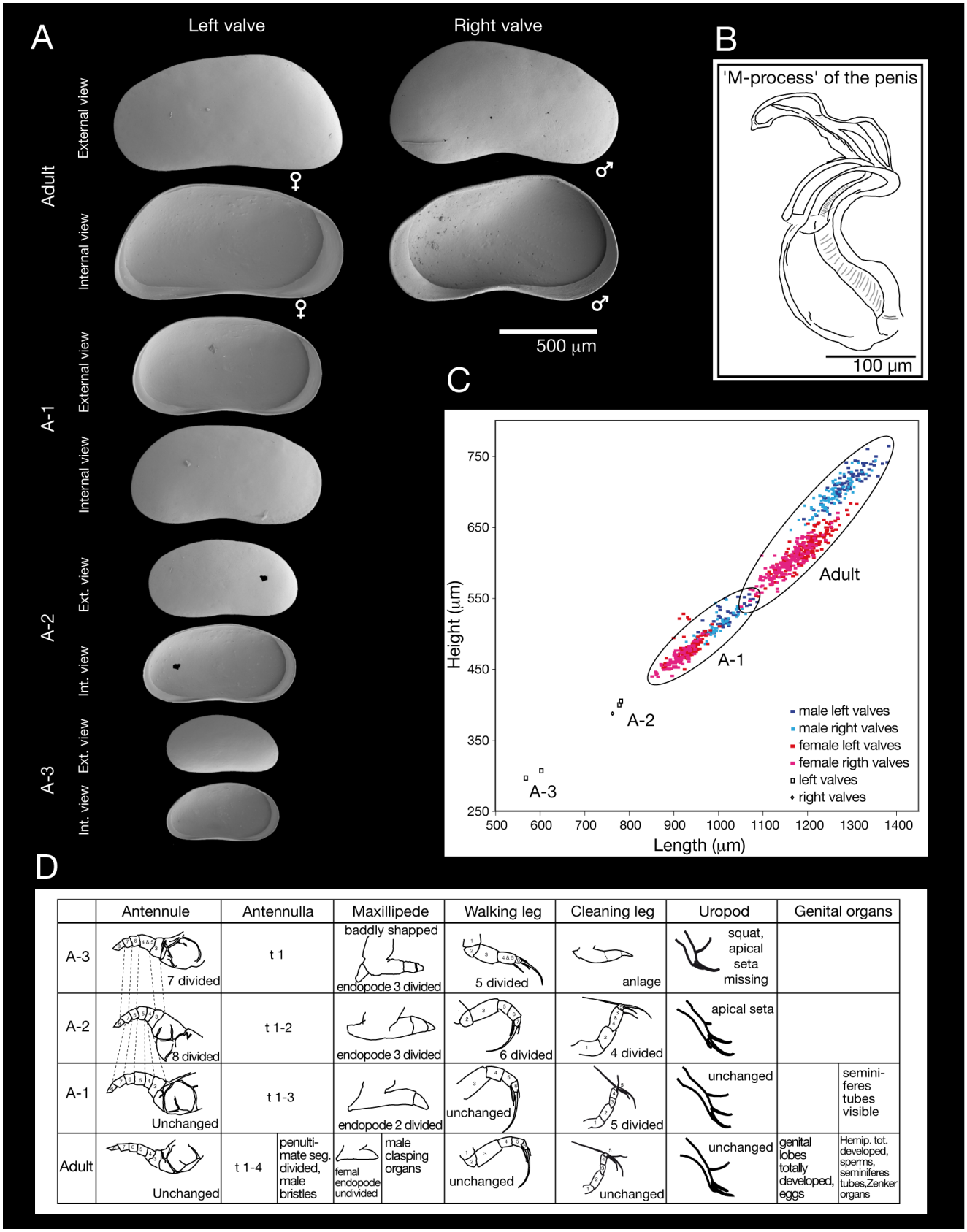


FIGURE 3.1
A) SEM photographs of adults and juvenile valves of *C. neglecta*, B) 'M-process' of the penis, C) valve size, D) ontogeny of the appendages from stage A-3 to adult.

TABLE 3.1
Monthly abundance (nbr. ostracods per core) and population density at 13, 33, and 70 m water depths.

site	sampling date	Total abundance	standard deviation	max	min	nbr. of cores	adult females	adult males	A-1 females	A-1 males	A-2	A-3	A-4
13 m	04.19.06	2.5	1.9	5	1	4	1.75	0.25	0.00	0.00	0.25	0.00	0.25
	05.10.06	1.0	0.0	1	1	2	0.50	0.00	0.00	0.00	0.00	0.00	0.50
	06.12.06	0.5	0.6	1	0	4	0.00	0.00	0.00	0.00	0.00	0.25	0.25
	07.11.06	11.0	5.7	15	7	2	0.00	0.00	0.00	0.00	6.00	4.50	0.50
	08.10.06	16.7	9.0	26	8	3	0.00	0.00	0.00	0.00	14.33	2.33	0.00
	09.12.06	11.7	7.1	18	4	3	0.00	0.00	0.00	0.00	11.67	0.00	0.00
	10.10.06	13.5	6.9	22	7	4	0.00	0.00	0.00	0.00	13.25	0.25	0.00
	11.15.06	4.0	6.1	11	0	3	0.00	0.00	0.00	0.33	3.67	0.00	0.00
	12.12.06	11.5	3.1	16	9	4	0.50	1.25	1.75	0.75	7.25	0.00	0.00
	01.16.07	14.0	5.3	19	7	4	3.75	2.00	1.75	1.00	5.50	0.00	0.00
	02.19.07	4.3	1.5	6	3	4	2.25	0.50	0.50	0.50	0.50	0.00	0.00
	03.27.07	4.5	3.7	9	1	4	2.75	1.25	0.25	0.00	0.00	0.00	0.25
	04.25.07	1.0	1.4	3	0	4	0.50	0.25	0.00	0.00	0.25	0.00	0.00
	annual population density = 7.4 ind./core (=2800 ind./m^2)						annual productivity = 12 ind.						
	annual maximum = 16.7 ind./core (=6300 ind./m^2)						net productivity = 1.71 ind./month						
33 m	04.25.06	5.0	1.4	7	4	4	0.50	1.50	1.00	0.25	1.50	0.25	0.00
	06.19.06	6.0	1.7	8	5	3	3.00	0.33	0.33	0.67	0.67	1.00	0.00
	07.25.06	3.3	2.9	7	1	4	2.00	0.25	0.50	0.25	0.25	0.00	0.00
	08.31.06	3.7	2.1	6	2	3	2.00	0.00	0.33	0.00	0.33	0.33	0.67
	10.04.06	3.3	1.5	5	2	4	1.50	0.00	0.00	0.00	1.00	0.50	0.25
	10.25.06	2.3	2.1	5	0	4	1.25	0.00	0.00	0.25	0.75	0.00	0.00
	11.28.06	4.3	0.5	5	4	4	0.50	0.00	0.00	0.00	2.00	0.50	1.25
	01.09.07	7.3	4.8	14	3	4	0.75	0.00	0.75	0.00	2.25	2.25	1.25
	02.15.07	10.0	6.1	16	3	4	0.00	0.00	0.25	0.25	5.75	2.25	1.50
	03.12.07	8.5	3.8	11	3	4	0.75	0.50	2.75	0.50	2.50	1.50	0.00
	04.10.07	8.5	3.0	11	5	4	0.50	0.75	1.25	1.50	2.50	1.50	0.50
	05.01.07	7.0	2.2	9	4	4	0.75	1.00	2.25	0.50	1.75	0.75	0.00
	annual population density = 5.74 ind./core (=2200 ind./m^2)						annual productivity = 14 ind.						
	annual maximum = 10.0 ind./core (=3800 ind./m^2)						net productivity = 1.23 ind./month						
70 m	04.19.06	6.8	2.9	10	3	4	0.25	0.25	1.00	0.25	1.25	2.00	1.75
	05.10.06	8.0	5.7	12	4	2	1.00	0.00	0.50	1.00	1.00	3.50	1.00
	06.12.06	8.0	4.2	11	5	2	2.00	1.50	0.00	1.00	2.00	1.50	0.00
	07.15.06	6.8	7.6	17	1	4	1.50	0.75	0.25	0.75	2.25	1.00	0.25
	08.23.06	18.5	19.1	32	5	2	2.50	4.50	2.00	2.00	7.00	0.50	0.00
	09.12.06	9.3	0.6	10	9	3	1.67	2.00	2.00	0.67	2.00	0.00	1.00
	10.10.06	8.0	4.7	12	3	4	2.50	2.00	2.00	0.00	1.00	0.00	0.50
	11.15.06	3.3	1.7	5	1	4	2.25	0.50	0.25	0.00	0.00	0.00	0.25
	12.12.06	3.3	1.7	5	1	4	2.25	0.50	0.25	0.00	0.00	0.00	0.25
	01.16.07	9.3	2.8	12	6	4	3.00	0.75	0.75	0.50	0.25	1.75	2.25
	02.19.07	8.0	4.2	13	3	4	1.75	0.75	0.50	0.25	1.75	1.50	1.50
	03.27.07	7.5	5.6	15	2	4	1.75	0.00	0.25	0.50	0.75	2.75	1.50
	04.25.07	7.5	3.7	11	3	4	0.25	0.50	1.00	1.00	1.50	2.50	0.75
	annual population density = 7.1 ind./core (=2700 ind./m^2)						annual productivity = 20 ind.						
	annual maximum = 9.3 ind./core (=3500 ind./m^2)						net productivity = 1.74 ind./month						

2. Results

2.1. Taxonomy and Ontogenesis of *Candona neglecta*

Identification criteria of the species belonging to the genus *Candona* are mainly based on the copulatory organ morphology. The shape of the "M-process" of the male penis (Fig. 3.1 B) is the most reliable diagnostic feature for *C. neglecta* (Danielopol, 1969; Meisch, 2000). The genital organs visible through the valve readily permit a distinction of males and females. Sexual dimorphism is also obvious for adults (Fig. 3.1 A), but is less marked in the last juvenile stage A-1. Although A-1 males are somewhat larger than A-1 females (Fig. 3.1 C), gender assignation relies on presence or absence of seminiferous tubules. Valve morphology and size (Fig. 3.1 A and C) permit to identify instars A-1 to A-4. Specific development of appendage of *C. neglecta* was studied from A-3 instar to adultness (Fig. 3.1 D) and identification of the juvenile stages confirmed using Henderson (1990). Identification of the juvenile stage A-4 was only based on valve shape and size, generally approximating 440 µm length (not shown here).

2.2. Population Density and Monthly Abundances

Only 1 male adult and 1 female adult were found at 5 meters water depth. In fact, except for these two specimens found during the winter period, all individuals of *C. neglecta* were collected at 13, 33 and 70 m in sandy to very fine organic rich sediment (substratum characteristic can be found in *Chapter IV*). Table 3.1 presents monthly individual abundances as well as population density of *C. neglecta* from April 2006 to May 2007 at 13, 33, and 70 m. Highest mean annual population density of *C. neglecta* is found at 13 and 70 m water depth (2800 and 2700 ind/m^2, respectively). At 33 m, the mean annual population density is reduced (2200 ind./m^2). Monthly individual abundances and monthly relative abundances are illustrated in Figure 3.2 for the three depths. Table 3.2 displays the monthly percentage of males and females for adults and A-1 juveniles.

Values at 70 m sampled on the 23rd of August 2006 are very high compared to the rest of the year. Due to strong winds during this day, only two cores could be taken. One of them had clearly been shaken and contained unusually high living ostracod abundances, suggesting that the core entered almost horizontally in the sediment and consequently sampled a much larger area. As the relative proportions of the different instars are not biased, both cores were considered, but the values were discarded for annual estimations.

TABLE 3.2
Monthly percentage of males and females at 13, 33, and 70 m water depths.

site	sampling date	% adult females	% adult males	% A-1 females	% A-1 males
13 m	04.19.06	88	13	0	0
	05.10.06	100	0	0	0
	06.12.06	0	0	0	0
	07.11.06	0	0	0	0
	08.10.06	0	0	0	0
	09.12.06	0	0	0	0
	10.10.06	0	0	0	0
	11.15.06	0	0	0	100
	12.12.06	29	71	70	30
	01.16.07	65	35	64	36
	02.19.07	82	18	60	40
	03.27.07	69	31	100	0
	04.25.07	67	33	0	0
33 m	04.25.06	25	75	80	20
	06.19.06	90	10	33	67
	07.25.06	89	11	67	33
	08.31.06	100	0	100	0
	10.04.06	100	0	0	0
	10.25.06	100	0	0	100
	11.28.06	100	0	0	0
	01.09.07	100	0	100	0
	02.15.07	0	0	50	50
	03.12.07	60	40	85	15
	04.10.07	40	60	45	55
	05.01.07	43	57	82	18
70 m	04.19.06	50	50	80	20
	05.10.06	100	0	33	67
	06.12.06	57	43	0	100
	07.15.06	67	33	25	75
	08.23.06	36	64	50	50
	09.12.06	45	55	75	25
	10.10.06	56	44	100	0
	11.15.06	82	18	100	0
	12.12.06	67	33	67	33
	01.16.07	80	20	60	40
	02.19.07	70	30	67	33
	03.27.07	100	0	33	67
	04.25.07	33	67	50	50

3. Discussion

3.1. Life-History of *Candona neglecta*

A quantitative approach, often including numerical simulation, is normally used to study population dynamics (see for example Geiger, 1990a). Such analyses are very difficult to perform given our sampling constraints because:

1) the number of replicate cores was low, which leads to low specimen abundances and a general inhomogeneity in the data;

2) only the last five development stages were separated and female fertility was not studied; and

3) no parallel laboratory culture was performed to assess development time and fertility.

Nevertheless, development trends are generally easy to discern and results appear to be conclusive.

Figure 3.2 illustrates that the life cycle of *C. neglecta* is different at the three sites. At 13 m, the development of the individuals from juvenility to adulthood is very easy to follow. Briefly, individuals of instars A-4 appear in spring and develop rapidly to reach instar A-2 at the beginning of summer. Thereafter, development stops and A-2 juveniles endure the warmest months as a dormant form with latent period (diapause). During the end of autumn and early winter, juveniles resume their development and moult promptly in A-1 stage and quickly reach maturity. By the end of winter, all individuals have reached adulthood. Development at 33 m is not as readily depicted. Development at this depth appears to be delayed and occurs over a longer period compared to the population living at 13 m. At 70 m, it is even more difficult to recognize a clear pattern. Monthly relative abundances of A-1 juveniles and adults present two peaks, suggesting that *C. neglecta* produces two generations at this depth. Because of the overlap between these peaks distinct cohorts are not clearly separable.

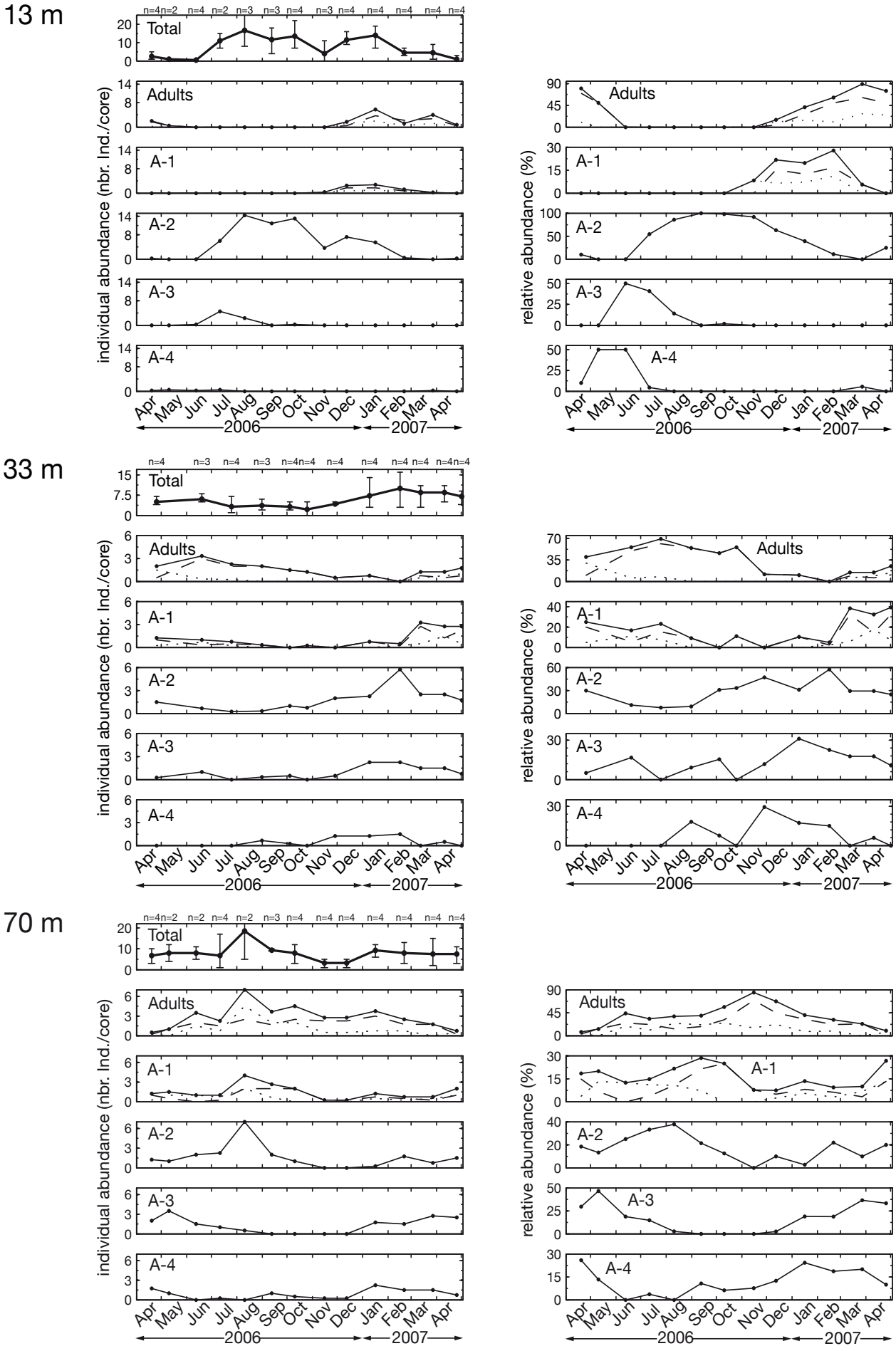


FIGURE 3.2
Monthly abundance (left graph) and monthly relative abundance (right graph) of *C. neglecta* at 13, 33, and 70 m. Dashed lines stand for females, dotted llines for males.

Three factors make the present diagrams difficult to understand:

i) The first and last points of the graph on the right are actually the same, both representing the month of April.

ii) The individual and relative abundances have to be represented. If only individual abundances were given the period of maximum development can be biased because the population is not always homogeneously distributed and, particularly if the number of samples is small, the results may not represent true development abundances. An example of this is given for the adult abundance recovered at 70 m. Maximum monthly abundance of adults was recovered in August (left graph), but this does not correspond to the maximum relative to the total abundances (right graph) but instead is related to a technical problem during sampling (see discussion above). However, using only relative abundances can also bias the interpretation. If, for example, individuals of one instar are dominant, this will also correspond to a maximum in the relative abundance even though it actually corresponds to a very low individual abundance. This should not be interpreted as the maximum of the development. Such a "biased" maximum can be seen for the adults collected in April 2006 at 13 m. The adults account for almost 90% of the total population but represent only about 2 surviving individuals originating from the development maximum one to two months before.

iii) The third factor is that the relative percentage of males and females is difficult to represent in Figure 3.

Using another way to illustrate the results may resolve these problems and help to depict the different patterns in development:

i) As the seasons have a cyclic characteristic, the graphs can be curved so that April 2007 represents the same point as April 2006, hence the graph forms a circle and the timing of population peaks are readily discerned.

ii) Both individual and relative abundance can be merged, in a more qualitative manner, together to get a more realistic judgement of the population dynamic. Thus, even if quantitative data are not clearly represented in the graph, the qualitative interpretation of both mean individual numbers and relative percentage to total population permit to evaluate the development of the species.

iii) Male and female percentages may be represented using colour patterns. Variations of the male:female ratio with time may be relevant in terms of population dynamics and reproduction behaviour and are, therefore, important to display.

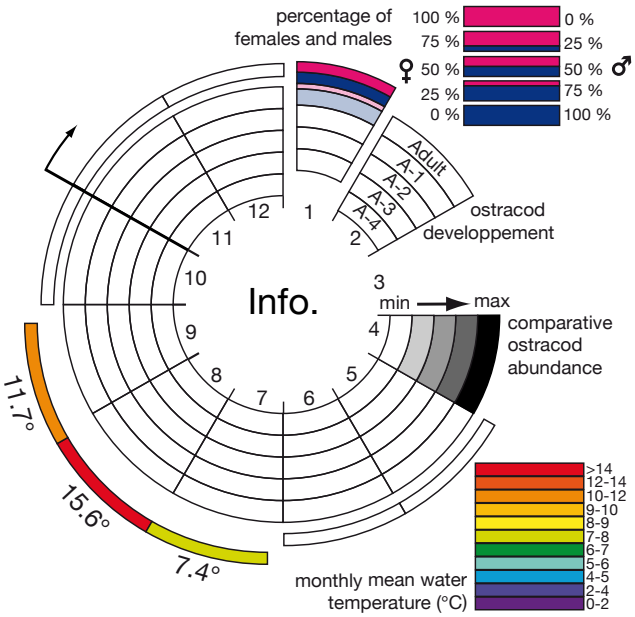


FIGURE 3.3
Construction of Synoptic Ostracod Watch Model (SOWM), see text for explanation.

Subsequently, we have developed a new qualitative method to represent phenology of the life history of ostracods.

3.2. Synoptic Ostracod Watch Model (SOWM)

In 1998, Külköylüoğlu used a watch dial to illustrate the seasonal occurrence of ostracods. In their presentations, December is placed at 12 o'clock, and each hour represents a month. Occurrence of the species is delimited by the angle defined by two hands. This innovative graphic was named Ostracod Watch Model (OWM). Here we apply an enhanced version of the OWM to illustrate not only the occurrence of individuals but also the juvenile development, the relative abundance and the male:female ratio as well as other secondary information such as water temperature, water depth, etc. The aim of this graphic is to display an overall and synthetic view of the life

cycle of the species. For these reasons, this improved version is called the Synoptic Ostracod Watch Model (SOWM). The construction of SOWM is shown in Figure 3.3. SOWM is also based on a watch dial; New Year (i.e. 1st of January) is placed at 12 o'clock. Each hour represents a month, January starts at 12 o'clock and finishes at 1 o'clock, February from 1 to 2 o'clock and so on. Months are noted in the middle of the dial using incremental month numbers (January = 1, February = 2, etc...). The circle is then divided into juxtaposed concentric bands; each band representing an instar, the outer band for adults, the second inner band represents A-1 juveniles, and so on up to the youngest juveniles, which are within the inner band. At this point, the dial is divided into boxes, each one representing an instar for 1 month. Each box is then filled with a grey scale corresponding to a 'comparative abundance'; white stands for no individual, black for maximal 'comparative abundance'. Here, 'comparative abundance' is a qualitative figure, deduced from monthly individual abundance and relative abundance that seeks to represent maximal development of the instar, i.e. the period when a maximum of individuals reach this development stage. In Figure 3.3, the white box in the inner band situated between 3 and 4 o'clock indicates that no A-4 individuals were found in April. Conversely, the black box of the outer band situated between 3 and 4 o'clock indicates that maximal development of adults took place in April. If the population is bisexual, the proportion of females and males can be illustrated with two sub-boxes by division of the initial box along its length. The inner box represents males and is coloured in blue, the outer box is coloured in red and represents females. The area of the sub-box is proportional to the percentage of each gender. Abundance of adult (males and females joint together) is represented by a change in the colour intensity of both colours (shading). In figure 3.3, the outer box between 12 and 1 o'clock shows that the maximum development of adults took place in January, and that at this time of the year the adult population consisted of about 50% of females and 50% of males. The box just underneath represents the abundance of the last juvenile stage A-1 in January and while it was large it is not yet the maximum. Also, during this month the males were more abundant than the females by about 3 males for 1 female (75% and 25% males and females respectively). An outer band, decoupled from the central watch dial can be used to represent different environmental parameters that influence ostracod development. In Figure 3.3, we have included monthly mean water temperature. The starting of the sampling period is represented with a bold line that in our case corresponds to early November. Other details, such as water depths, type of environment, authors of the study, etc. can be also inserted in the middle of the dial. More symbols can be added to the model to enrich the illustration or to improve its general comprehension. On the other hand, SOWM can also be adapted and simplified to illustrate limited or sparse data taken from the literature.

Naturally, this type of representation is only qualitative and may be a rather subjective interpretation ideally suited to represent initial results. Nevertheless, irrespective of the type of data and the manner they are illustrated, SOWM can be extended to allow for a comparison of results from different studies. Moreover, the fact that it is easy to read and yet includes abundant information that is represented in a synthetic way using very little space, justifies the use of SOWM to display the ostracod life history. However, the data must be accessible, in tables or non-printed data repositories, in order to verify the interpretations and/or use the data for more quantitative studies.

3.3. Life-Cycle of *Candona neglecta* Using SOWM

13 meters water depth: The life cycle of *C. neglecta* in Lake Geneva is illustrated using SOWM in Figure 3.4. The general trend of the development at 13 m has already been discussed above. However, some particularities stand out when the results are illustrated using SOWM. The first individuals to reach stage A-1 and maturity are males, suggesting that males develops faster than females during at least the last two moults. Consequently, a high proportion of males are present at the start of moulting from A-2 in A-1 and from A-1 to maturity. Afterward, females appear and out-number slightly males. At the end, only females are found, and this for both A-1 juveniles and adults. The summer diapause of A-2 juveniles lasts approximately 4 months and moulting in the next stage (A-1) occurs only when water temperature drops to below 12 °C. Adults appear when water temperature is less than 9 °C. Last adults are found in water with a temperature of 8.2°C. One month later, monthly temperature reaches 12°C and no adults were found, suggesting that maximal surviving temperature of adults in Lake Geneva is approximately 9°C. The adult development maximum is found in March, development from stage A-4 to maturity last at minimum 8 months for precocious individuals and generally 11 months for the greater part of the population.

33 meters water depth: At 33 m the life cycle of *C. neglecta* is less evident compared to that at 13 m. Development is delayed and appears to be stretched out over the year. First A-4 individuals appear in

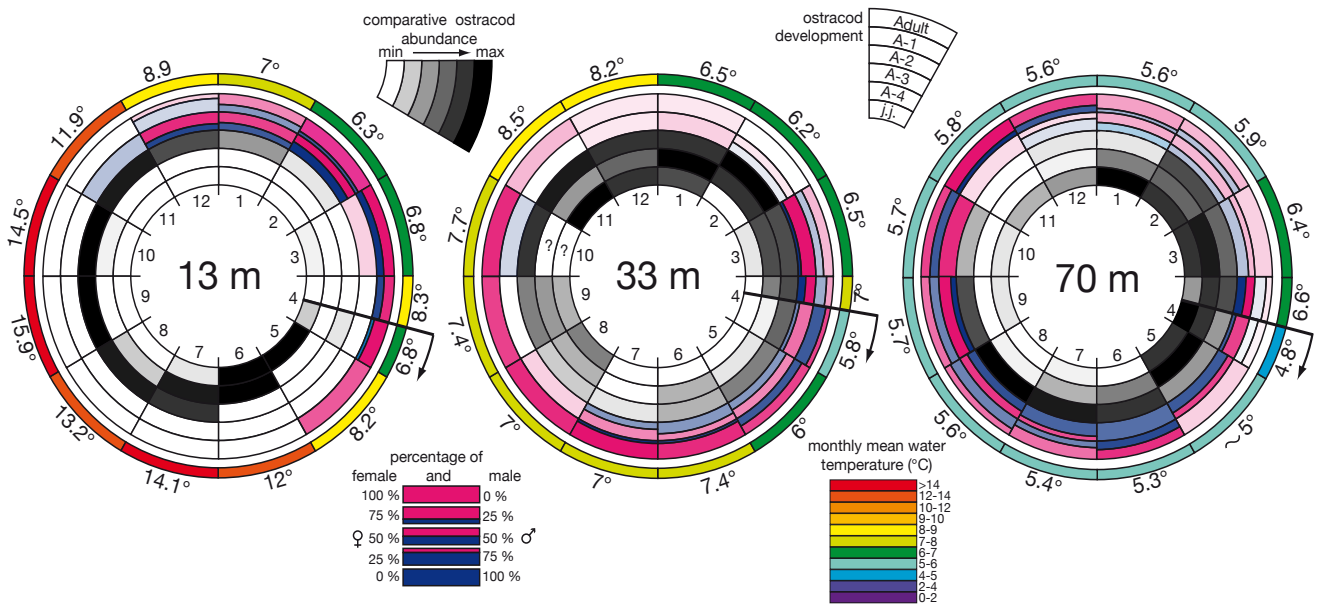


FIGURE 3.4
SOWM of *C. neglecta* at 13, 33, and 70 meters water depths.

August and develop constantly to reach maturity after 8 months in March. These precocious individuals only account for a part of the population. Effectively, most of the individuals reach stage A-4 in November and adulthood in April and May. Last A-4 individuals present in January reach maturity in June and July. For most of the individuals, development from stage A-4 to adult lasts approximately 6 to 7 months. All individuals belong actually to the same cohort but differences in their rate of development results in the spread. Thus, slowly developing individuals and surviving adults can be found until winter, i.e., 7 to 8 months after the maximum of the development that occur in April-May. As at 13 m depths, males are dominant at the beginning of maturation but are quickly outnumbered by females that survive much longer. Development at 33 m is much faster than at 13 m. But as the diapause lasts approximately 4 months, 'effective' development at 13 m equals that at 33 m.

70 meters water depth: The monthly relative abundance exhibits two maxima for adult and last juvenile stages A-1 and, in a less visible way, for younger juveniles, suggesting that two generations arise during the year (Fig. 3.2). The SOMW shown in Figure 3.4 supports this interpretation with two maxima easily depicted for the juvenile stages. Moreover, this type of representation permits to show proportions of males what may help to point at the appearance of freshly moult A-1 juveniles and adults. The term of "generation" or "cohort" is problematic here because they are linked to a particular concept. Development of one generation, or more precisely of one cohort, contains all steps, from the hatching of eggs to copulation and consecutive laying of eggs. Thus, the next generation (or cohort) originates from the eggs laid by the previous generation. It is also possible, though, that the eggs can have been by laid by a previous "generation". In this case, the generations overlap in time. For example, *Loxoconcha elliptica* has one generation per year that is apparently split into two (Heip, 1976; Horne, 1983). For this reason, the term "population" of individuals will be used instead of generation or cohort. The two populations of individuals can be followed during their respective development. For the "first" population, the maximum of individuals of stage A-4 occurs in January. These individuals reach maturity in June and July. For the "second" population, the maximum of individuals of stage A-4 occurs in April, and maturity is reached in October and November. In a general view, development from stage A-4 to adulthood lasts 7 to 8 months. For both populations, males outnumber the females at the very beginning of the moulting period (up to several months before the maximum) of the last juvenile stage A-1 (March and June-July). This short predominance of males is less well expressed for adults because adult females survive longer and mask the arrival of the freshly moulted males and this reduces the proportion of males. Nevertheless, at the beginning of the main moulting period of adults (April and August), proportions of males are higher (see Table 3.2). Adults, principally females, can be found throughout the rest of the year. These individuals most probably represent surviving specimens from the second population and/or, specimens that developed slower and reached maturity later.

For all depths, specimen abundances are relatively low (Fig. 3.2 left) and thus the question of representativeness of the results has to be addressed. Calculating statistical significance is probably not helpful in this case because the population is too inhomogeneous, with very high variations of the number of specimens between cores. For example, for one sampling session, one core may contain 17 specimens and the next one only one. In such a case, deviation from average is enormous and the significance of the value is very low. However, summing the different results from the retrieved cores increase the sampled area what in turn decrease spatial variation. With these results, significance has no real meaning and no statistical tests were done. Nevertheless, at 13 m, the pattern of the development is very clear. This is not the case at 70 m, where the significance of the observed peaks has to be questioned, especially because only relatively small temporal variations can been seen. If the peaks are not significant as they result from sample inhomogeneity, then *C. neglecta* only produces one generation per year. This latter stretches over nearly all the year, and females lay eggs almost continuously but that hatch without clear timing. Quality of our results is not sufficient to exclude this hypothesis. There are different reasons for this: firstly, it is not easy to distinguish if the two peaks of A-4 and A-3 juveniles are really two distinct maxima or if it is only one maximum that occurs earlier than that of the previous year. This is especially difficult to resolve because the short lapse of time between the two peaks occurs exactly at the beginning and end of the survey (Fig. 3.2 right). A study including younger juvenile stages and, more importantly, conducted over a longer period of time could invalidate the presence of two distinct hatching episodes. Secondly, double peaks can only be seen in the relative abundance but are not discernable in individual abundance (Fig. 3.2). Studying the number of eggs in females and taking more replicate cores (8 or more cores) to get more homogenous and representative figures would certainly help to validate the reality of two periods of maturity during the year.

Nevertheless, there is some support for a real change in population structure. Firstly, the maxima can be followed from one instar to the other, suggesting that the peaks are not randomly distributed but dictated by the development of the animal. Secondly, long hatching periods are clearly unfavourable because predation would become more important. Accordingly, it is advantageous to have one synchronous and brief period of hatching occurring one or more times per year. Thirdly, variations amongst the proportions of males are consistent with the two maxima of relative abundance of A-1 juveniles and, to a lesser degree, of adults (see above), suggesting that there are two peaks of moulting. Given that these peaks correspond to two development maxima, one interpretation would be that *C. neglecta* produces two generation (cohorts) per year with the adults of the first one giving birth to the second. Populations producing two generations per year are common for ostracods and have already been mentioned for *C. neglecta* (Alm, 1915; Wolf, 1920). However, this interpretation is unlikely for Lake Geneva as A-4 instars of the second group appear in April only, while the first group has not yet attained maturity and is consequently not able to reproduce. Hence, the eggs are from a previous generation. In this case, the two groups overlap in time and develop in an intercalated manner. Thus, for each group, only one generation is produced per year and the two populations may be referred as sub-generations. For the reasons cited above, the hypothesis of two groups intercalated in time and developing one generation per year is favoured, but the hypothesis of one generation (cohort) only occurring at different intervals over the year cannot be excluded either.

3.4. Male to Female Ratio

At all depths males are predominant at the beginning of the moulting period. A brief predominance of males and variations of the male:female ratio through time has already been described for *C. neglecta* (Wolf, 1920; Meisch, 2000), and is also common in other Candoninae (Hartwig, 1901; Alm, 1915; Hiller, 1972; Mallwitz, 1984) as well as other ostracods species (Theisen, 1966; Kamiya, 1988; Schön and Martens, 1998). The predominance of males at the beginning of the moulting period may be related to a faster development during the last two periods of moulting, with males reaching maturity slightly before females. This behaviour may be linked to a competition copulation strategy, because the first males that are able to copulate have a higher chance to reproduce. In contrast, females live longer than males, which will influence the reproduction processes. The longer life span of females will bias the male:female ratio of the population with females being over-estimated. It is thus difficult to give a representative figure of gender repartition. For a comparison with previous studies, a yearly average is thus considered as the most viable approach. For adults the male:female ratios are as follows: 1:2.1, 1:3.1, and 1:1.6 at 13, 33 and 70 m depths, respectively. For the last juveniles the ratios are: 1:1.6, 1:2.3, and 1:1.4 at 13, 33 and 70 m, respectively.

For sexual reproduction, a ratio of 1:1 would be expected. Lower proportions of males in the adult population can be explained by the longer life span of females and the timing of the sampling. A shorter life span of males can be related to higher predation linked to copulation behaviour (Fenwick, 1984; Kamiya, 1988). Males have to actively search for mates and therefore will explore outside of their relatively protected microhabitat within the sediment. This is supported by differences in the carbon isotopic compositions of adult valves that reflect a last moulting of males in a distinct microenvironment compared to that of females (*Appendix 1*). Males are hence more exposed, which may increase their loss by predation (Mbahinzireki et al., 1991; Uiblein et al. 1992). In addition, males also have to develop their genital organs, which are large compared to their body size and requires an increase in carapace size during the last three moults (Fig. 3.1 C; Heitkamp, 1979). This process will consume a very high amount of energy and may also increase mortality during moulting in comparison to females. The bias of the male:female ratio described in the literature is, in general, higher (ranging from 1:2 to 1:4) than in Lake Geneva (Alm, 1915; Hiller, 1972; Meisch, 2000). Differences in this ratio could simply be related to the timing of sampling or in fact support a lower mortality of males in Lake Geneva as a result of better environmental conditions and/or a lower concentration of predators.

3.5. Population Density

Data about the population density of *C. neglecta* are rare in the available literature. The littoral and deepest zones of large lakes commonly represent stable and/or predictable environmental conditions for which low species abundance, low fecundity and long life cycles are expected (Geiger, 1998). This is especially the case for deep oligotrophic lakes (Griffiths, 1993). A rudimentary comparison of Candoninae population of large deep great oligo- or mesotrophic lakes such as Loch Ness (Griffiths, 1993), Great Slave Lake (Tressler, 1957) and Lake Pääjärvi (Holopainen and Paasivirta, 1977) indicates that the population density in Lake Geneva is higher. The population of *C. neglecta* in the Bothnian Bay is, however, much higher, ranging from 3000 to 38,000 Ind./m^2 with an estimated average of 7700 Ind./m^2 (estimated from Fig. 1, p. 70 in Savolainen and Valtonen, 1983). The coastal area of the Baltic Sea experiences a high load of nutrients (Rheinheimer, 1998), which increases the food availability for benthic organisms in the Bothnian Bay. In addition to other suitable environmental factors (water temperature, sediment texture, predation), the abundant availability of nutrients favours *C. neglecta* as long as the water is sufficiently oxygenated.

Density population of *C. neglecta* in Lake Geneva can be classified as intermediate and may reflect the mesotrophic level along with a good oxygenation of the basin. Within Lake Geneva, the best way of comparing population size is to examine the annual number of females (annual productivity) and number of females per productive month ('net productivity'; Table 3.1). Annual productivity is: 12, 14, and 20 females (nr. females/core) at 13, 33, and 70 m depths, respectively. Productivity is comparable at 13 and 33 m but higher at 70 m. Hence, a population producing two populations per year generates a larger amount of females and thus a higher population density over one year. The 'net productivity' is: 1.71, 1.23 and 1.74 (nr. females/core/productive month) at 13, 33 and 70 m of water depth, respectively. Values at 13 and 70m are comparable, because productivity is very high during a few months at 13 m. In contrast, values at 33 m are always low, but at 70 m they are always high. This means that both sites at 13 and 70 m are similar in terms of resource availability and can support equal population densities. The site at 33 m is a less favourable habitat for *C. neglecta*.

Sediment characteristics, organic matter proportion and water chemistry are, however, very similar at 33 and 70 m depths, but totally different at 13 m (*Chapter IV*). Consequently, the repartition of *C. neglecta* is not directly affected by substrate, organic matter proportion or water chemistry. The sites at 13 and 70 m are, however, located on the SE shore of the basin while the station at 33 m depths is set on the SW side of the same basin. In the "Petit-Lac" the SE shore is well protected and the fetch effect of the dominant wind direction is relatively low. In contrast, the SW shore is well exposed to the northerly wind (the "bise") and consequently the fetch effect is high (Girardclos, 2001). Material reworking and turbidity and thus the sedimentation style and organic matter recycling within the water column is expected to be strongly influenced by the "bise" at the 33 m depth station. The present dataset, however, does not allow us to exclude other causes such as different types of organic matter sources, competition, higher predation, higher levels of pollution in the sediment, etc. Variation with depth of the entire ostracod population density is discussed in more detail in a companion paper (*Chapter III-2*).

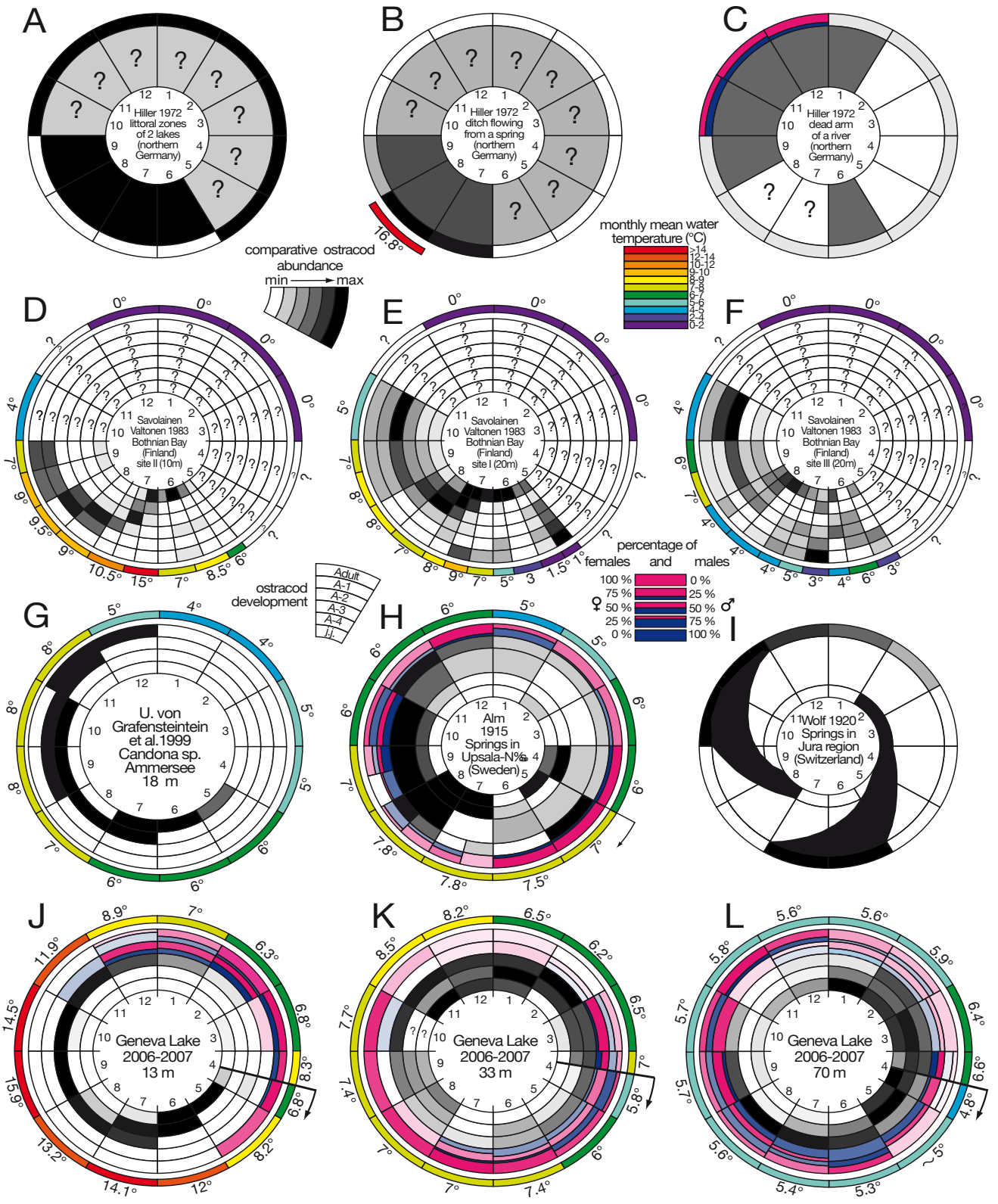


FIGURE 3.5
Life cycle of *C. neglecta* and Candoninae from different studies illustrated using SOWM. Data from: Hiller (1972; A, B & C), Savolainen et Valtonen (1983; D, E, and F), von Grafenstein et al. (1999b; G), Alm (H; 1915), Wolf (I; 1920) and present study (J, K, and L).

3.6. Comparison of Life-Cycles of *Candona neglecta* in Different Habitats

Specimens of *C. neglecta* have been found in a number of diverse types of environments, including brackish environments, springs, ponds, brooks connected to springs, pools, ditches, streams, littoral and deep zones of lakes, underground water, and in temporary waters. This capacity to adapt to different environments characterizes its ecology: oligothermophilic

but with a tolerance for a temporary increase in temperature beyond 20°C, oligo- to mesorheophilic, titanoeuryplastic and/or polytitanophylic, euryplastic for pH, mesohalophilic, perhaps polyhalophilic (see Meisch, 2000 for a complete review). Results of five studies on the temporal distribution of juveniles and adults conducted in central and northern Europe (Alm, 1915; Wolf, 1920; Hiller, 1972; Savolainen and Valtonen, 1983; von Grafenstein et al. 1999b) are illustrated using SOMW in comparison to the present results in Figure 6. Other studies describing the life cycle of *C. neglecta* in a less detailed way are not represented in figures here. Nüchterlein (1969) studied the freshwater ostracoda fauna in the region of Franken (Germany) and found juveniles of *C. neglecta* throughout the year, with the population reaching maturity at the end of winter to early spring. Rieradevall and Roca (1995) presented monthly abundance of *C. neglecta* in a karstic lake in Spain. In the study, juveniles were not distinguished from adults and the authors concluded that, the ostracods have a non-seasonal life-history.

What strikes at first is the bimodal repartition of the life cycle of *C. neglecta*. All life cycles can be classified in two types of development: one with one generation per year and another with two generations per year. The sites studied by Hiller (Fig. 3.5 A, B and C), the shallower site studied by Savolainen and Valtonen (Fig. 3.5 D), the littoral zones of the Ammersee and Starnberger See (Fig. 3.5 G), and the sites at 13 and 33 m in Lake Geneva (Fig. 3.5 J and K) typically host populations of *C. neglecta* producing one generation per year. All theses sites represent relatively shallow water depths and have large variations in temperature. Temperatures, when data are available, reach at least values of 8 to 9°C at one time of the year. In all sites, except the ditch studied by Hiller (1972), only juveniles are found during the warmer month and adults reach maturity when water temperature decreases. This supports that juveniles of *C. neglecta* can tolerate higher water temperatures compared to adults, surviving the summer up until the adult stage is reached while temperatures decrease. The occurrence of adults at 16.8°C in the ditch studied by Hiller (1972) is surprising and difficult to explain. The specimens could have been transported from another habitat. Or these specimens may have survived from spring to summer.

For sites with larger water depths and in springs, *C. neglecta* produce two generations per year (Fig. 3.5 H and I) or two sub-generations (Fig. 3.5 L). Life cycles at 20 m described in the Bothnian Bay (Fig. 3.5 E and F) resemble those described by Alm (1915) in a spring with adults at two distinct periods of the year, suggesting that *C. neglecta* produce two generations in the Bothnian Bay. That would imply that the population has to develop an entire generation during winter and spring in water temperatures reaching freezing point and eggs must have been laid before mid-summer. Some ostracods enter torpidity when placed on ice or placed in cold water (Delorme and Donald, 1969; Xia et al. 1997). Thus, it is plausible that specimens of stages A-2, A-1 and adults enter torpidity in autumn and wait until temperatures increase during the end of spring to resume their development, actually representing another type of diapause. If this is the case, these two sites can be classified as having one generation per year only. Nevertheless, in the springs studied by Alm (1915) and Wolf (1920), there are clearly two populations that reach maturity at distinct times. The authors interpreted that both populations correspond to two distinct generations. It is possible that the two generations described by Alm (1915) and Wolf (1920) are actually also only one generation per year split into two "sub-generations" but this cannot be confirmed.

In summary it emerges that *C. neglecta* is able to produce two generations, or two "subgeneration" when seasonal variations are small with temperature ranging from 4 to 8°C. Groundwater springs and deep areas of lakes typically provide such stable habitats with very low variations of physico-chemical conditions and temperature. If higher seasonality is the case, *C. neglecta* produce only one generation, often with a diapause to survive high or very low water temperature. To conclude, *C. neglecta* adapts its life cycle as a function of the thermal dynamics of the habitat.

What can also been observed on the SOMW is that the two "sub-generations" found in Lake Geneva are regrouped to form an asymmetric pattern in comparison to the temporal symmetry described in springs. Both juvenile maxima are regrouped in winter and spring and both adult maxima are regrouped in summer and autumn. This timing for juvenile appearance is perhaps the result of mixing of water during winter. In the Ammersee and Starnberger See, younger juveniles of *Candona levanderi* and *Candona candida* appear just after the first mixing of the water column when oxygen level is the highest (von Grafenstein et al., 1996). Even if the deep water of the "Petit-Lac" is well oxygenated during the whole year, higher values are reached at the beginning of the year (CIPEL, 2006), which may influence the timing for the hatching and development of the larvae. Timing of adults may be related to nutrient availability. Primary production in the epilimnion depends on the water temperature and hours of sunshine, thus the flux of sinking organic

matter during the warmest month provides elevated food supplies for the last steps of the development of ostracods in the abyssal area of Lake Geneva.

Mezquita and co-authors (2005) calculated the optimum and tolerance parameters, including water temperature, for many species. Values for *C. neglecta* are 2.23 ± 1.6, 20.59 ± 1.99 and 10.7 ± 1.6 °C for the mean January temperature, mean July temperature and annual temperature, respectively. These figures are attributed to the whole population, including juveniles, adults, and diapause period. Thus, when only adults are discussed, values are greatly overestimated. A similar study by Viehberg (2006) in northeast Germany took additionally into account the species phenology. For this study, samples were used only when adult and A-1-instars were simultaneously collected to assume moult activity and so the ecological optimum. The models estimated an optimum temperature of 7.6 °C for *C. neglecta* with a tolerance of 2.2°C. Our results based on living ostracods are in good agreement with these estimations. In addition, *C. neglecta* developed a stable population during at least several hundreds of years (Decrouy, *non published data*) in the deepest part of the "Petit-Lac" where temperatures fluctuated between 5°C to 6 °C with periodic extremes of 4°C and 7°C (CIPEL, 1984; CIPEL, 2006), corroborating values assessed for this species by others.

In almost all the sites studied development lasts some 3 to 4 months, at maximum 5. This rapid development contrasts strongly with the slow development found in Lake Geneva and Ammersee. Rapidity is primordial in the shallower sites of Bothnian Bay because females must lay eggs before water temperature reaches 0°C. Fortunately, water temperature increases at these depths during summer, which accelerates the metabolism and permits faster development and calcification (Geiger, 1990a; Roca and Wansard, 1997). In deeper water, development is generally slower but precocious adults are already found in autumn. In these areas, population density is high but very few adults are found in comparison to the youngest juveniles, suggesting that mortality is very high (data from Savolainen and Valtonen, 1983). This high mortality is certainly due to the rapid development, with ostracods undergoing the risks of early moulting before the winter rather than not being able to reproduce before the coldest period of the year. High fertility and rapid development that induce high mortality permits *C. neglecta* to colonize these harsh habitats. The rapid development in springs described by Alm (1915) and Wolf (1920) is perhaps advantageous in environments that are stable in terms of temperature and chemistry but that undergo regular external perturbation such as strong current or mixing of the sediment induced by meteorological extremes or animals. Under these conditions, mortality is in any case high. It is thus favourable to have a large population that develops and reproduces rapidly. In our study, population density is low but adult abundances are approximately equivalent to juvenile abundances, suggesting that mortality is much lower. In deep water, perturbation of the habitat is very rare and there is no need to attain maturity quickly. Food resources, on the contrary, are low. In these conditions, it is advantageous to develop slower in order to reduce mortality during moulting. As a consequence, more individuals reach maturity and reproduction is assured. A high fertility is also not necessary, as too many individuals would exhaust the food resources

In summary, the results of our study comprising the seasonal sampling of contrasting settings indicate that *C. neglecta* is able to modify its population dynamics in order to accommodate to changing environmental conditions in its habitat. A careful documentation of the causes behind these changes in population dynamics in a modern natural system such as Lake Geneva is critical in order to improve the use of ostracods for palaeoenvironmental reconstructions.

Chapter III - 2 :

RECENT OSTRACODS IN LAKE GENEVA (SWITZERLAND): PART II. AUTOECOLOGY AND POPULATION DYNAMICS

1. Introduction

Ostracods are good environmental markers because the presence or absence and/or the abundance of most species is very sensitive to environmental conditions. In addition, the low-Mg calcite valves of ostracods are well preserved in sediments and hence can be used, together with their geochemical compositions, as sensitive tracers for palaeoenvironmental studies. However, precise knowledge on the ecology of ostracod species is required before the shells can be used to interpret past environmental conditions (Danielopol et al., 1985, 1993; Geiger, 1993; Schwalb, 2003; Belis and Ariztegui, 2004; Viehberg, 2006). Ecological features of a specific species can also vary from one place to another (Hiller, 1972; *Chapter III-1*). Site-specific population dynamics, bathymetric distribution and microhabitat preferences are, among others, important when dealing with fossil ostracods. Unfortunately, information on specific species is often scarce, placing limits on the interpretations.

This is particularly the case for many central European lakes, most notably the larger lakes in Switzerland, where little work has been done in terms of ostracod classification since the early studies of Wolf in 1920. Furthermore, for Central Europe biggest lake, Lake Geneva, the last detailed studies date back to the work of Kaufmann (1896), and this despite the historical importance of the lake for the field of limnology (Forel, 1900). More recent studies using ostracods from lake sediments for palaeoclimatic reconstructions of Lake Zürich and Lake Neuchâtel, respectively, were made by Lister (1988) and Schwalb and co-authors (1994). Unfortunately, despite the success of these studies, the interest in studies of ostracods in Switzerland did not increase markedly. Besides, many major environmental changes occurred during the 20th century, affecting aquatic habitats and leading to a drastic change in ostracod communities. Consequently, data recovered by former ostracodologists are now outdated but permit to measure the effect of environmental changes.

In this study, the main ecological features of living ostracods from the "Petit-Lac" ("small lake", western basin) of Lake Geneva, are illustrated and discussed. This study is the biological contribution to a broader project attempting to reconstruct palaeoenvironmental changes in Lake Geneva using ostracods. Detailed studies of the geochemistry of living ostracods as well as of ostracods separated from short cores are in progress (*chapter V-1* and *V-2*). This study will form the basis for an interpretation of climatic-environmental changes since the last deglaciation.

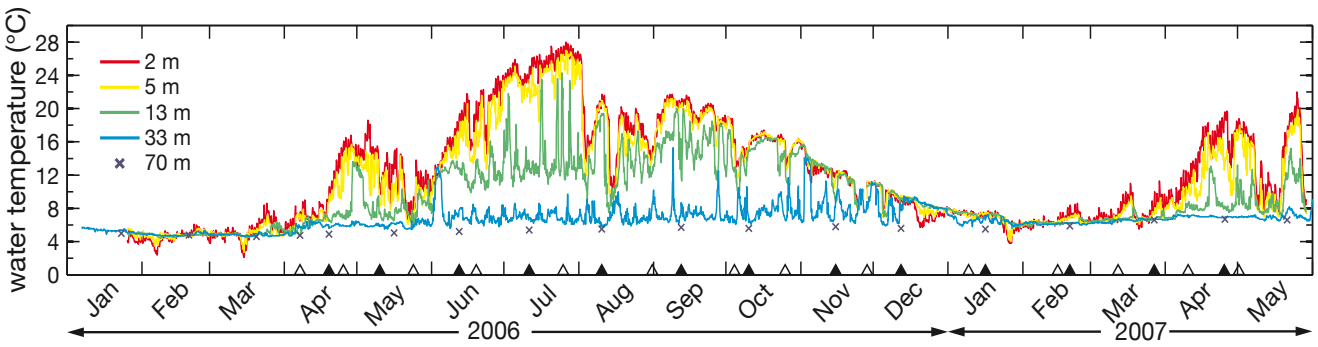


FIGURE 3.6
Water temperature measured at the five sampling sites from January 2006 to May 2007. Empty triangles stand for dates when stations at 2, 5, and 33 m depths were visited, in-filled triangles stand for the stations at 13 and 70 m depths.

TABLE 3.3
Synthetic characteristics of the five sampling sites.

water depth	sediment type and texture	grain size	H_2O (%)	$CaCO_3$ (%)	TOC (%)	vegetation	fauna
2 m	Large banks of pebbles and rather limited beds of coarse sand sittuated in depressions	pebbles and coarse sand	-	-	-	macroalga and macrophytes from end spring to end autumn	- lots of zebra mussels, gammaridae and asellus aquaticus, some gasteropodes, pisidium, limnea, planaria and trichoptera larva
5 m	Substratum of medium sized sand punctuated by isolated pebbles sometime groupped in banks	middle sized sand and pebbles	-	-	-	macroalga and macrophytes from end spring to end autumn	- lots of zebra mussels, several gammaridae, asellus aquaticus, and gasteropodes (of which Bithynia tentaculata), some pisidium, limnea, planaria and trichoptera larva
13 m	Intercalation of large zebra mussel mats and beds of middle sized sand	silty sand	85%	62%	1.4%	mostly no vegetation apart alga and plant residu	- large beds of zebra mussels - in the sand: some chironomids and pisidium sp. and few gammaridae and gasteropods
33 m	Very fine sediment, very rich in water with a high organic matter content, having a "jelly-like" texture	clayed silt	93%	45%	2.9%	no vegetation	lots of copepods and many chironomids
70 m	Very fine sediment, very rich in water with a high organic matter content, having a "jelly-like" texture	clayed silt	95%	44%	3.3%	no vegetation	lots of copepods and many chironomids

2. Results

2.1. Environmental Parameters

2.1.1. Physical and chemical evolution of water

During the sampling period, water temperature varies from 2.1 to 28°C (Fig. 3.6). Lowest values were measured during the fairly cold winter 2005-2006. Summer 2006 was characterised by an unusually warm July and an abrupt cooling at the beginning of August. Autumn 2006 was abnormally warm and the winter 2006-2007 exceptionally mild. Early spring 2007 was also exceptionally warm with record temperatures for the month of April. Water temperature at 2, 5 m and, with a certain delay, at 13 m depths directly parallels the air temperature. In addition, temperature at 33 and 70 m increases continuously during this unusually warm year and is only slightly lowered during winter 2006-2007.

2.1.2. Substratum and sediment texture

Table 3.3 summarises the different characteristics of the different substratum, sediment, and fauna found at the five sampling sites.

2.2. Ostracoda Fauna

2.2.1. Ostracod systematic

A total of 16 species were recovered alive (Plate 1 and 2). Species are listed above according to their taxonomic rank; the species marked with an asterisk (*) were only found as fossils in the sediment cores.

Superfamily Cypridoidea s. str. Baird, 1845
  Family Candonidae Kaufmann, 1900
    Subfamily Candoninae Kaufmann, 1900
      Genus *Candona* s. str. Baird, 1845
        - *Candona candida* (O.F. Müller, 1776)
        - *Candona neglecta* Sars, 1887
      Genus *Fabaeformiscandona* Krstić, 1972
        - *Fabaeformiscandona caudata* (Kaufmann, 1900)
        - **Fabaeformiscandona* cf. *protzi* (Hartwig, 1898)
      Genus *Pseudocandona* Kaufmann, 1900
        - *Pseudocandona compressa* (Koch, 1838)
      Genus *Cryptocandona* Kaufmann, 1900
        - **Cryptocandona reducta* (Alm, 1914)
    Subfamily Cyclocypridinae Kaufmann, 1900
      Genus *Cypria* Zenker, 1854
      - *Cypria ophtalmica* forma *lacustris* (Jurine, 1820)
  Family Ilyocyprididae Kaufmann, 1900
    Subfamily Ilyocypridinae Kaufmann, 1900
      Genus *Ilyocypris* Brady & Norman, 1889
      - *Ilyocypris* sp.
  Family Cyprididae Baird, 1845
    Subfamily Eucypridinae Bronshtein, 1947
      Genus *Prionocypris* Brady & Norman, 1896

- *Prionocypris zenkeri* (Chyzer & Toth, 1858)
Subfamily Herpetocypridinae Kaufmann, 1900
Genus *Herpetocypris* Brady & Norman, 1889
- *Herpetocypris reptans* (Baird, 1835)
Subfamily Isocypridinae Rome, 1965
Genus *Isocypris* G. W. Müller, 1908
- *Isocypris beauchampi* (Paris, 1920)
Subfamily Cypridopsinae Kaufmann, 1900
Genus *Cypridopsis* Brady, 1867
- *Cypridopsis vidua* (O.F. Müller, 1776)
Genus *Plesiocypridopsis* Rome, 1965
- *Plesiocypridopsis newtoni* (Brady & Robertson, 1870)
Genus *Potamocypris* Brady, 1870
- *Potamocypris similis* G.W. Müller, 1912
- *Potamocypris smaragdina* (Vávra, 1891)
Superfamily Cytheroidea Baird, 1850
Family Limnocytheridae Klie, 1938
Subfamily Limnocytherinae Klie, 1938
Genus *Limnocythere* s. str. Brady, 1867
- *Limnocythere inopinata* (Baird, 1843)
Genus *Limnocytherina* Negadaev-Nikonov, 1967
- *Limnocytherina sanctipatricii* (Brady & Robertson, 1869)
Genus *Leucocythere* Kaufmann, 1892
- **Leucocythere mirabilis* Kaufmann, 1892
Family Cytherideidae Sars, 1925
Genus *Cytherissa* Sars, 1925
- *Cytherissa lacustris* (Sars, 1863).

2.2.2. Ecological features

Figure 3.7 B displays the bathymetric distribution and relative abundance of living ostracods. Population density is illustrated in Figure 3.7 C. Figure 3.8 displays life histories of the dominant species belonging to the Family Candonidae using SOWM. Figure 3.9 represents life histories of the more important species belonging to the Family Cyprididae and to the Superfamily Cytheroidea. Ostracod penetration depths are shown in Figure 3.10.

The specific bathymetric distribution, life history, habitats and penetration depth of the different species are presented in *Appendix I.*

3. Discussion

3.1. Bathymetric Distribution and Population Density

In the following subsections, we examined, at first, the distribution of the population in term of species number and individual abundance as well as a possible relationship between environment and reproduction modes. The subsequent sections take in account the specific biological characteristics of the different species and discussion was centred on the environmental factors that can influence the abundance of the ostracods.

3.1.1. Species numbers versus individual abundance

Bathymetric and spatial distributions of ostracods in large water bodies have already been presented in numerous publications (Löffler, 1969; Kempf and Scharf, 1980; Danielopol et al., 1985, 1993). Major parameters that influence spatial distribution (at the same depth) are substratum, food supply and probably predation (Jungwirth, 1979; Benzie, 1989). For depth distributions temperature and oxygen concentration are the main parameters (Yin and Geiger, 1995). The distributions of ostracods in Lake Geneva are very similar to those in Lake Constance (Löffler, 1969), but also to those of Lake Laacher (Kempf and Scharf, 1980) and Lake Mondsee (Danielopol et al., 1993; Yin and Geiger, 1995). In general, the maximum in species richness and specimen abundance occurs in the littoral and sublittoral zone. A decrease in specimen abundance as well as species richness is observed between 13 and 33 m depths, that is just underneath the sublittoral zone. The number of species continues to decrease with depth but specimen abundance increases slightly beyond 33 m. This pattern is typical for mesotrophic lakes: optimal oxygen abundance and prevailing food conditions in parallel with habitat richness characterise littoral areas, while beneath the thermocline (i.e. approximately 15 to 20 m in the studied area) harsher conditions prevail due to changes in physical condition and/or supply of organic matter as nutriment and/or predation increases. At even greater depths conditions often change for the better with higher amounts and/or better preservation of organic matter accumulating in zones with lower oxygen content (Yin and Geiger, 1995).

3.1.2. Parthenogenetic versus bisexual population

Distribution of the species is also related to their reproductive modes. Geiger (1998) affirms that wind-exposed littoral zones of lakes favour parthenogenetic species because such environments undergo important environmental changes that are not predictable. In unstable environments but where the changes are predictable (for example water temperature) and in true stable environments, bisexual populations are advantaged. For Lake Geneva, the fetch effect on the south-eastern shore (sites at 2 and 5 m water depths) is particularly high whereas it is low in the Bay on the south-western shore (site at 13 m depths) (Lehmann,

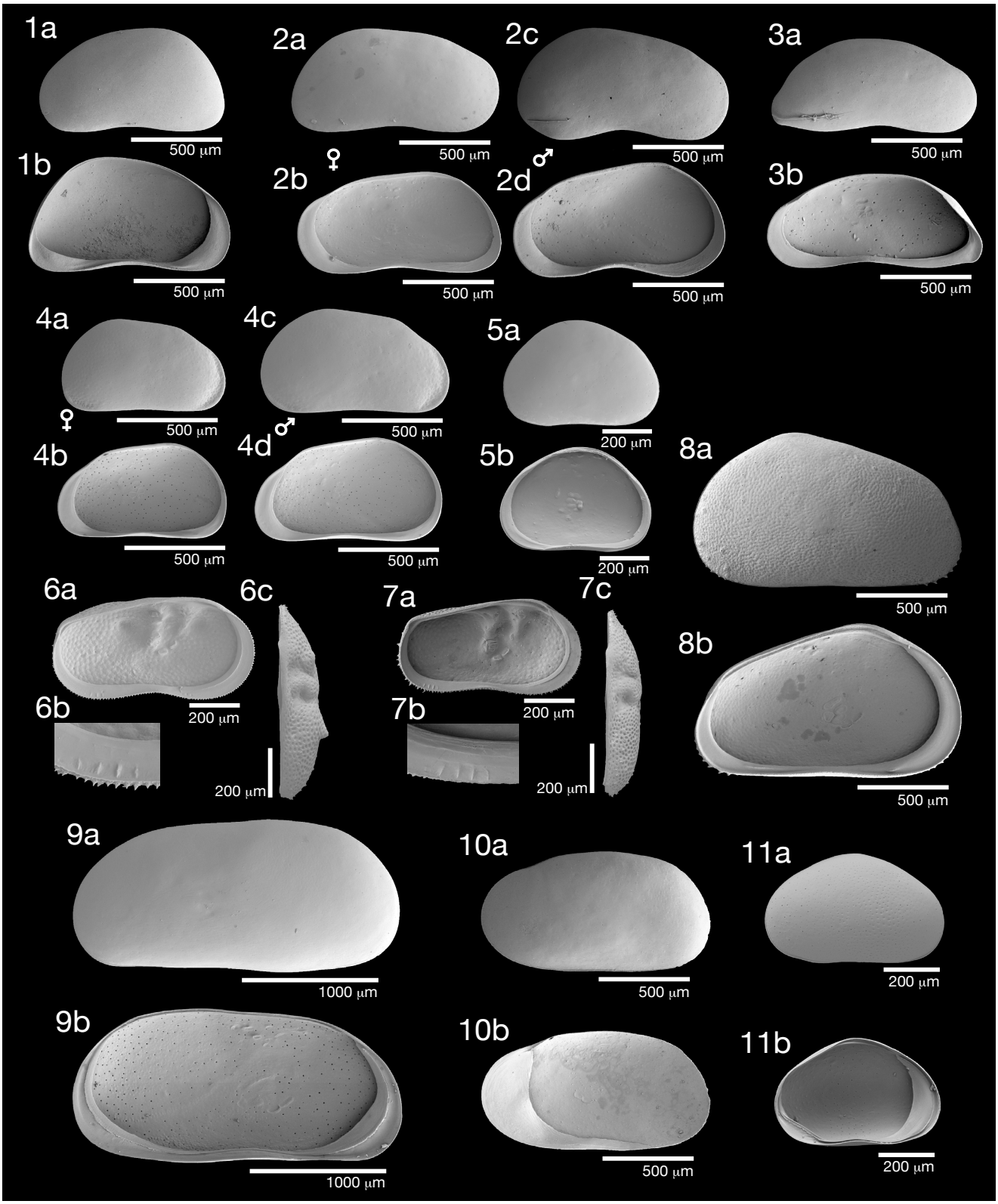


PLATE 1
SEM photographs of adult valves: (1 a and b) *Candona candida* (2 a and b); *Candona neglecta* female, (2 c and d) *Candona neglecta* male; (3 a and b) *Fabaeformiscandona caudata*; (4 a and b) *Pseudocandona compressa* female, (4 c and d) *Pseudocandona compressa* male; (5 a and b) *Cypria ophtalmica*; (6 and 7 a, b, and c) *Ilyocypris* sp; (8 a and b) *Prionocypris zenkeri*; (9 a and b) *Herpetocypris reptans*; (10 a and b) *Isocypris beauchampi*; (11 a and b) *Cypridopsis vidua*.

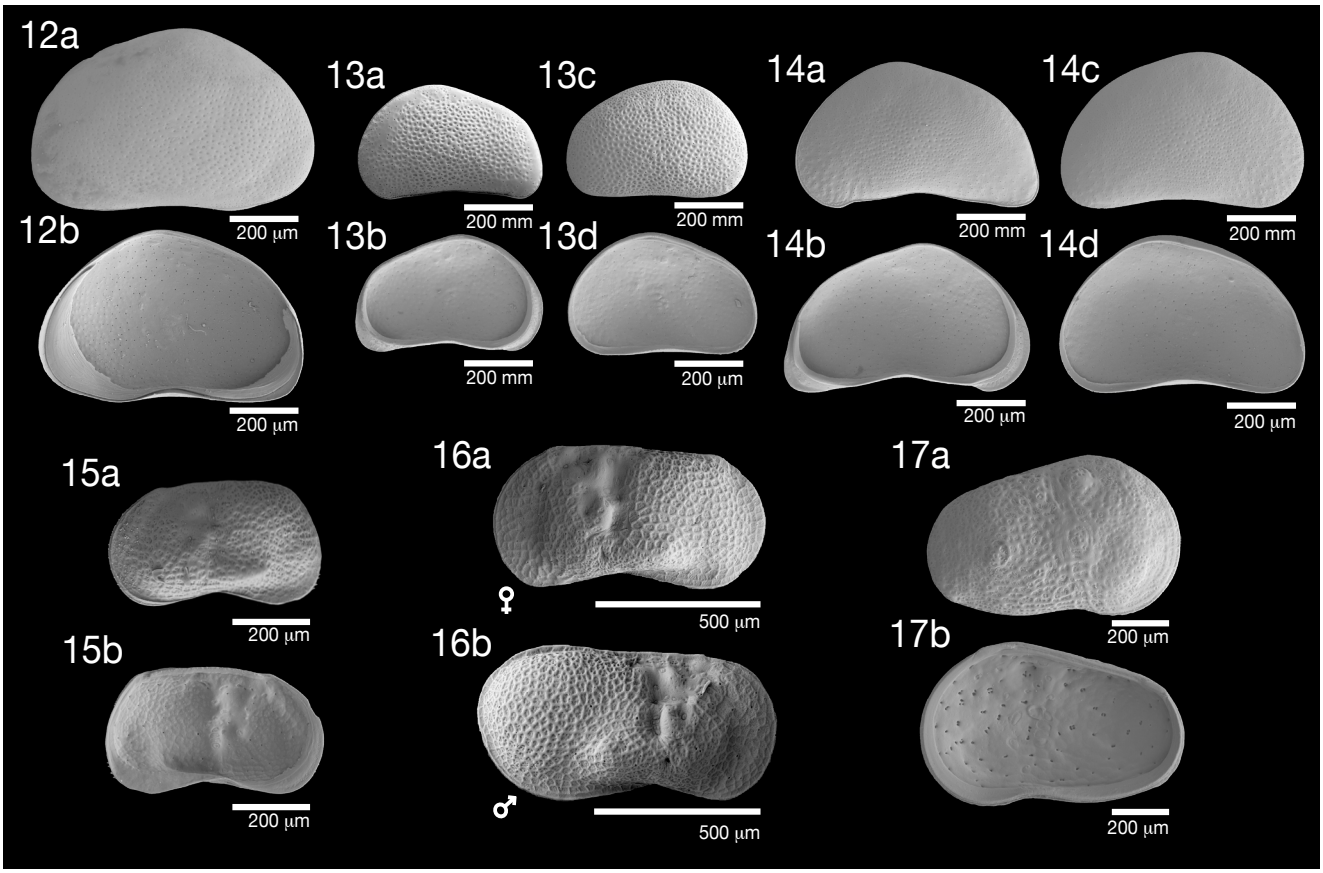


PLATE 2.
SEM photographs of adult valves: (12 a and b) *Plesiocypridopsis newtoni*; (13 a, b, c, and d) *Potamocypris similis*; (14 a, b, c, and d) *Potamocypris smaragdina*; (15 a and b) *Limnocythere inopinata*; (16 a) *Limnocytherina sanctipatricii* female; (16 b) *Limnocytherina sanctipatricii* male; (17 a and b) *Cytherissa lacustris*.

1998). In all three sites, changes in temperature are significant but sites at 2 and 5 m experience rapid and not predictable, short-term changes that are related to wave currents, whereas the site at 13 m is characterized by more predictable, longer-term changes in temperature. The above-cited model predicts that the two shallow sites are dominated by parthenogenetic forms whereas the sites at 13 m and deeper are dominated by bisexual species. This is, to some extent, observed because at the two shallow sites, of the 9 species present, only 1 is bisexual while at 13 m, only 3 of 9 are bisexual. The most profound site is typically a very stable environment and hosts effectively 2 bisexual species for 1 parthenogenetic species, the latter being particularly well adapted to a deep and cold habitat (Fig. 3.7).

3.1.3. Water Temperature

Water temperature is an essential factor limiting the dispersion of ostracods. Many species need a specific temperature range to develop and reproduce successfully. Hence, their geographical and/or bathymetric distribution is strongly controlled by temperature.

Most littoral species (*Ps. compressa*, *C. vidua*, *Pl. newtoni*, *P. similis*, *P. smaragdina*, and *L. inopinata*) rank in the mesothermophilic to warm stenothermal forms and are summer form and/or reach maturity during the warm season (Meisch, 2000). Thus, water temperature may limit these species to the littoral zone where water temperature is warm in summer. Of these species, only *Limnocythere inopinata* was found deeper, i.e. at 13 m depth, and may therefore be somewhat more tolerant to cooler temperature. Nevertheless, its occurrence at this depth is restricted to the summer month (see below) and its abundance remains rather low. Oxygen isotope compositions of the valves indicates that adults moult at a minimum temperature of 10.5°C but more generally between 14 and 18 °C (*Appendix I*). At 13 m, water temperature jumped from 8 to 12 °C in June 2006 and remained relatively constant until the end of October (Fig. 3.6). The depth dispersion limit in Lake Geneva for this species must approximately be around or just below 13 m. This species is considered to be restricted to shallow waters, but was already noted in other locations in deeper water (Sywula, 1977; Savolainen and Valtonen, 1983), indicating that under favourable conditions (see also below) it can inhabit

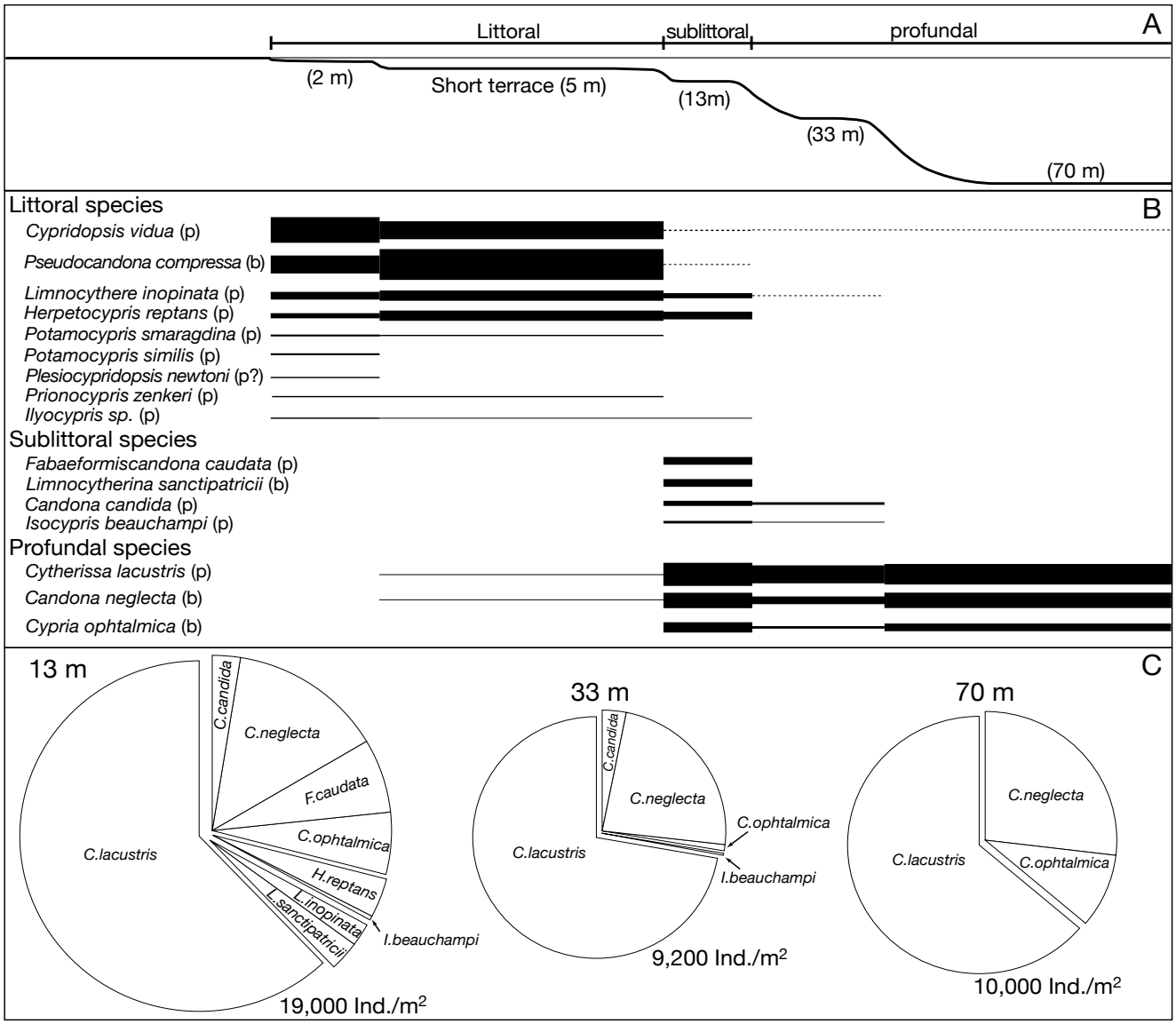


Figure 3.7
(A) Simplified morphology of the studied zone, (B) Relative non-quantitative abundance of each species at the different sampling sites: (p) symbol stand for parthenogenetic form and (b) symbol for bisexual form, thickness of bold line correspond to relative abundance, and dashed lines stand for reworked living specimen, (C) Population density at 13, 33, and 70 m depths.

somewhat deeper waters if temperature permits this. However, it is not clear if *L. inopinata* establishes a permanent population at this depth. Presence of different juveniles stages together with adults, as well as geochemical evidences suggest that the specimens moult in place. Nevertheless, younger larvae may have been reworked from the littoral zone and established themselves during a tolerable temperature period. Successful reproduction at this depth has, therefore, still to be proven. *H. reptans* is the only littoral species that ranks in the thermoeuryplastic (Meisch, 2000) and other factors than water temperature must therefore determine its bathymetric distribution.

In contrast, sublittoral and profundal species occur mostly in the cold stenothermal to oligothermophilic forms (*C. candida*, *C. neglecta*, *F. caudata*, and *L. sanctipatricii*) or in the eurythermal form with preference to cold water (*C. lacustris*). Hence, they are expected to occur only in deep sites where temperature remains constantly cold or increases only slightly during summer. (For the last case, the animals can adapt their life-cycle to 'survive' the warmest period (see below)). One species ranks in the polythermophilic form (*C. ophtalmica*) but is frequent and well adapted to deep zones of lakes. Surprising is the occurrence of a warm stenothermal species (*I. beauchampi*) at 13 and 33 m depths. In the previous studies, this species occurs only in the littoral zone of lakes (Meisch, 2000). Its occurrence in relatively fresh water in Lake Geneva, even if its abundance is very low, suggests that its temperature tolerance may be larger and its restriction to littoral zone in other lakes related to other factors than temperature. As these

last two species (*C. ophtalmica* and *I. beauchampi*) would tolerate and even prefer warm temperatures, their absence in the sublittoral zone must results from other factors than temperature such as predation and/ or competition (see also below).

3.1.4. Energy level, substrate, and nutriment

Wave current strength, and thus energy level, decreases with depth, resulting in a very diverse type of substratum (see Table 3.3). As benthic organisms, ostracods find their food in/on the sediment or on the algae (which are only present in littoral zone where energy level is high), these three factors are strongly interdependent.

Both littoral sites are very similar in terms of physico-chemical parameters and substratum type. In both sites, dense populations of macrophytes and macroalgae (Lehmann, 1998), provide grazing surfaces and shelter for phytophylous species (Roca et al, 1993; Uiblein et al., 1996) and direct and indirect food for herbivore and detritivore species in both sites (Benzie, 1989). This similarity is reflected by the presence of identical species. Nevertheless, the two sites differ in terms of wave current frequency and strength. Whereas the site at 2 m water depths is continuously affected by wave currents, the site at 5 m is only affected temporarily during windy periods (Girardclos, 2001). This difference seems to affect species specimen abundance: phytophylous species are able to swim (*C. vidua*, *Pl. newtoni*, *P. similis*, *P. smaragdina)* and are more abundant in the shallower site whereas benthic species that can only crawl and dig (*Ps. compressa*, *L. inopinata*, and *H. reptans*) are more abundant in the deeper and thus quieter site. This suggests that the ability to swim is an advantage to the first group where wave currents are permanent and strong whereas the presence of non-disturbed sand beds at 5 m depth provides a habitat for the second group at 5 m depths. However, these species cannot profit from the sand beds at 2 m depth because they are frequently disturbed. Nevertheless, they can benefit from pebbles that are covered with algae, which provide a rough surface where detritus is caught up and organisms can crawl over, substituting sand beds as both food sources and microhabitat.

In deeper sites, energy level is very low and the substrate consists mainly of totally undisturbed silty-sand to clayed silt. At these depths, all species live directly on or in the sediment. This latter serve both as protection and as food dispenser. This substrate type suit perfectly to the habitat preference of *C. lacustris*, a typical profundal species that is mainly found in fine-grained sediments and which prefers silty fine sand sediments (10-100 µm) to coarse sandy substrate (500-100 µm) and very fine sediment (<10 µm) (Powell, 1976 cited in Carbonel et al., 1988; Danielopol et al, 1990a, 1990b).

Two typical littoral species (*H. reptans* and *L. inopinata*) were collected in this type of habitat at 13 m. Habitat and food preferences are well known for both species. In Lake Neusiedler, *L. inopinata* prefers fine, organic matter-rich sediment, and calm water (Jungwirth, 1979). From field observations and laboratory cultures, Benzie (1989) suggested that this ostracod prefers faecal material as a food source and a sandy habitat. In Loch of Strathbeg, *H. reptans* showed a positive association with faecal pellets and wood debris; in laboratory experiments, fine sediment was preferred as substrate; old macrophytes and old macroalgae were the preferred nutriments even though the species can survive on a wide range of food (Benzie, 1989). Besides, this species seems to be strongly affected by predation (Whatley, 1983). Thus, even if no macroalgae nor macrophytes grow at this depth, this site presents a good balance for these two littoral species between the sand that provides a suitable micro-habitat and shelter from predation, nutriments from the shore (terrestrial and lacustrine plant remains) and faecal pellets, both abundant in the sediment. In addition, *H. reptans* was collected in the Lake Constance down to a depth of 15 m (Löffler, 1969), suggesting that favourable substrate type, food availability, and low predation may permit the establishment of this species in sublittoral zones.

3.1.5. Oxygen availability and sediment texture

Oxygen is vital for ostracods and yet each species has need of a different oxygen level, leading to dispersions of the species. The “Petit-Lac” is well oxygenated throughout the year because of the annual overturn in winter and the mixing induced by wind. Oxygen availability decreases with depth: the littoral zone is permanently oxygenated, while the sublittoral (13 m depth) zone has lower values during summer with minimal values of 9 mg/l, and the profundal zones (33 and 70 m depths) have the lowest values of approximately 7 mg/l (personal communication, SECOE). Oxygen availability is also important for the preservation of organic matter and hence the availability of nutriments for ostracods. Therefore, ostracod population can be directly affected by oxygen concentration or indirectly by a change in their microhabitat or the nutriment supply.

From experimental studies, some species are known to be very sensitive (*I. beauchampi* and *L. inopinata*) or relatively sensitive (*C. vidua* and *Potamocypris* sp.)

or relatively tolerant (*C. lacustris*, *C. neglecta*, and *C. ophtalmica*) to a temporal reduction of the oxygen levels (Geiger 1990b; review in Meisch, 2000). The depth dispersion limit of *I. beauchampi* as well as *L. inopinata* may in part be explained by a lower tolerance of oxygen availability. The high tolerance to low oxygen concentrations of *C. lacustris*, *C. neglecta*, and *C. ophtalmica* explains in part the dominance of these species in the sublittoral and profundal zones.

The importance of higher or lower oxygen supplies for a species may also be deduced from its penetration depth in the sediment. As oxygen concentrations decrease with depth in the sediment, species with a need for higher oxygen levels have a more superficial habitat (see section 3.4). Lower oxygen availability and/or sediment textures with lower effective porosity may explain the low abundance or even absence in the deeper zones of *C. candida* and *L. sanctipatricii*, both having shallow sediment penetration depth a 13 m (see below).

3.3. Faunal Evolution with Special Considerations for the 20th Century

Early studies effectuated during the beginning of the 20th century and first results on short core studies (*Appendix I*) permit an evaluation of the evolution of the profundal ostracod fauna in the "Petit-Lac" during approximately the last 2000 years.

3.3.1. First century to end of 19th century

During the last 2000 years, 20th century excepted, the faunal assemblage is dominated by *C. neglecta* and *C. ophtalmica*. *C. neglecta* is particularly well adapted to the profundal zones of Swiss lakes and can be found throughout the Holocene (Schwalb et al., 1998; Lister, 1988). During the last 1500 years, the population of *C. neglecta* has remained very stable in profundal zones of Lake Neuchâtel (Lambert, 1999). In the "Petit-Lac", *C. neglecta* was found in sediments of Allerød age and throughout the Holocene (Anadón et al., 2006). Whereas the population of *C. neglecta* was very stable during this period, abundance of *C. ophtalmica* was higher during the Middle-Age Climatic Optimum. Minor species include *L. sanctipatricii*, *Leucocythere mirabilis*, *Cryptocandona reducta, Fabaeformiscandona protzi* and *Ilyocypris* sp. Abundances of these species follow the inverse pattern compared to *C. ophtalmica*, *i.e.* abundances were higher during the end of the Early Subatlantic period and during the Little-Ice Age. These minor species are known to prefer colder waters and are very sensitive to environmental degradation whereas *C. ophtalmica* is a very tolerant species in terms of environmental conditions and temperature variations (review in Meisch, 2000). Sedimentary and geochemical studies of the sediment suggest that primary productivity remains fairly constant until end of the 19th century. Therefore, temperature more than primary productivity level must have controlled ostracod population changes during this period.

3.3.2. Twentieth century

As for many other European Lakes, both basins of Lake Geneva suffered from anthropogenic nutriment overload at the end of the 19th and during the 20th century. Whereas this led to severe deep water anoxic episodes in the "Grand-Lac" (eastern basin), the "Petit-Lac" (western basin) remained well-oxygenated, with oxygen concentrations generally between 8 and 11 mg/l (min 6.04 mg/l in 2002), even during maximum phosphate overload (data from SECOE, personal communication). Still, due to higher primary productivity, the sediment became finer-grained, darker, with a larger amount of authigenic calcite and higher organic matter content. Beside, due to the 20th century global climate warming, water temperature of deep water of the "Petit-Lac" increased gradually to reach mean values of around 6-7°C (data from SECOE, personal communication).

Changes in the deep ostracod community of Lake Mondsee due to water eutrophication were particularly well studied. There, the first species to disappear from the profundal zone is *L. mirabilis* and it is followed by *F. caudata*, *L. sanctipatricii*, and *C. lacustris*. Last species to disappear are *F. protzi*, *C. ophtalmica*, and *C. neglecta* (Danielopol et al., 1985).

Total extinction of ostracods in the deep water of the "Grand-Lac" during the anoxic period can be assumed to be mostly identical to that which has been observed in Lake Mondsee. Faunal evolution in the "Petit-Lac" is similar to the faunal evolution described above. Short core studies and early work done on ostracods in Lake Geneva (Kaufmann, 1896; Forel, 1900) indicate that *L. sanctipatricii*, together with *Leucocythere mirabilis*, had a wider distribution and could be found in deeper sites before the 20th century. These two species, together with *C. reducta* and *F. protzi* disappeared progressively from the profundal zone of the Petit-Lac during the 20th century as in other lakes. These species are known to be very sensitive to degradation of water quality and disappeared from numerous lakes or deep zones of lakes due to increasing anthropogenic effects (review in Meisch, 2000). Quasi-disappearance of

L. sanctipatricii and probable total-extinction of *L. mirabilis*, *C. reducta* and *F. protzi* are probably related to the 20th century anthropogenic nutrient overload and/or general warming of the deep water due to global climate change. For this study, living specimens of *L. sanctipatricii* were only found in the site at 13 m depths, suggesting that this species, together with *F. caudata*, which reacts in a similar way compared to *L. sanctipatricii* with regard to a change in the environment (Danielopol et al., 1985), found shelter in this site.

More interesting are the differences between the evolution observed in the Mondsee and that observed in the "Petit-Lac". Whereas *C. lacustris* disappeared early in the eutrophication process of other large lakes, this species previously only sporadically present in the "Petit-Lac", colonised the deeper zones of the basin and quickly dominated the entire ostracod population. Löffler (1975, 1978) noted that an early disappearance of *C. lacustris* was directly related to a change in sediment texture, which in turn relates to a higher amount and hence better preservation of organic matter due to lake eutrophication and declining oxygen concentrations. This species has a relatively low respiration rate (Newrkla, 1985) and is able to survive temporal hypoxic conditions (Geiger, 1990b) but required an oxygen concentration of at least 3 mg/l to establish a permanent population (Delorme, 1978; Geiger, 1993). Geiger (1990b) suggested that not only oxygen depletion but also the long development time, the endobenthic lifestyle, and low active migration explain the disappearance of this species in Lake Mondsee. Today, *C. lacustris* is the dominant species in the "Petit-Lac" from the sublittoral to the deepest zones (Fig. 3.7 C). Sediment texture, slight decrease of oxygen concentration, and/or global warming may have disfavoured the very sensitive species such as *L. mirabilis* and *L. sanctipatricii* but favoured *C. lacustris*, which may be more resistant to oxygen depletion and/or have a different need in terms of microhabitat and food. *C. lacustris* may have even profited from the additional nutrient supply. While a slight increase of the specimen number is also noted for *C. neglecta* and *C. ophtalmica*, their increase is small compared to that of *C. lacustris*.

This situation concerning the relative proportions of *C. lacustris*, *C. neglecta*, and *C. ophtalmica* and changes thereof, has also been observed for Lake Neuchâtel (Lambert, 1999). This lake generally presents the same characteristics as the "Petit-Lac", with an anthropogenic nutrient overload that leads to an increase in primary productivity during the 20th century but having well-oxygenated deep water. More detailed studies on ostracod communities in such well-oxygenated lakes may help to understand how the different species are affected by eutrophication and environmental changes. Lake Geneva, with its two contrasting basins, would be the ideal place for such a study.

3.4. Life History and Population Dynamics

Horne (1983) reviewed life-cycles of Podocopids. The author stated that temperature is generally regarded to be the main factor controlling periodicity in the life-cycle of ostracods and that another important factor, food supply, may be closely related to temperature. He also noted that competition amongst species may also be an important criterion. The SOMWs in Figures 3.8 and 3.9 clearly show that development of most of the species is controlled by water temperature and that the life-cycle can vary from one site to another. The littoral zone is dominated by species having a rapid development and being only present during the warm months. Those species have a short life-cycle because they need to complete their total life-cycle before the return of colder conditions. *Ps. compressa* is the only species with a life-cycle lasting 1 year. This species overwinters as a dormant form with a latent period (diapause). In the sublittoral zones, species adapted to colder conditions with life-cycles of 1 year or more dominate. These species survive warmer month as a dormant form (diapause) and terminate their life-cycle during winter. Two species, *L. sanctipatricii* and *L. inopinata*, have short life-cycles. These species have very restricted temperature tolerance and can only develop during a short lapse of time: winter and spring for the former, summer and autumn for the latter. In deeper zones, temperature varies only slightly and species adapted to the cold with life-cycles of 1 year or more can develop continuously. At 33 m, the temperature variations are not insignificant and seasonality can still be observed even if the development is spread over time (*C. neglecta* and in a less clear way *C. lacustris*). At 70 m, temperature is almost constant and can not be an important constraint for ostracod development. *C. lacustris*, for example, shows no seasonality at this depth. But *C. neglecta* and, although less clear, *C. ophtalmica* both present a seasonal life-cycle. Other seasonal factors such as food availability linked to primary productivity in the epilimnion and/or variations of oxygen concentrations in deep water may control the seasonal development of these two species.

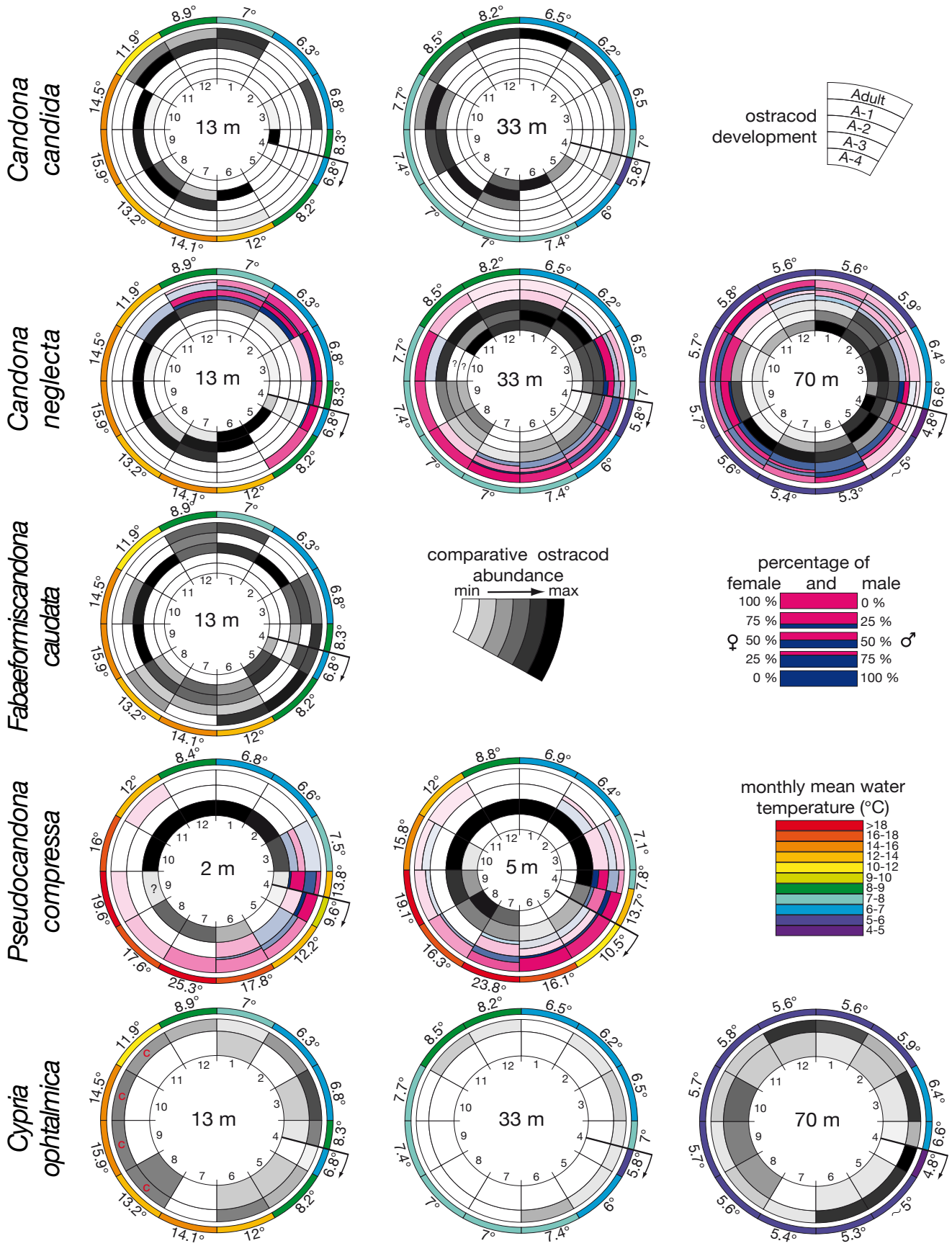


FIGURE 3.8
Life-cycle of the species belonging to the Candonidae Family using SOWM. The red «C» symbolise period of moulting deduced from oxygen isotopic composition (see text).

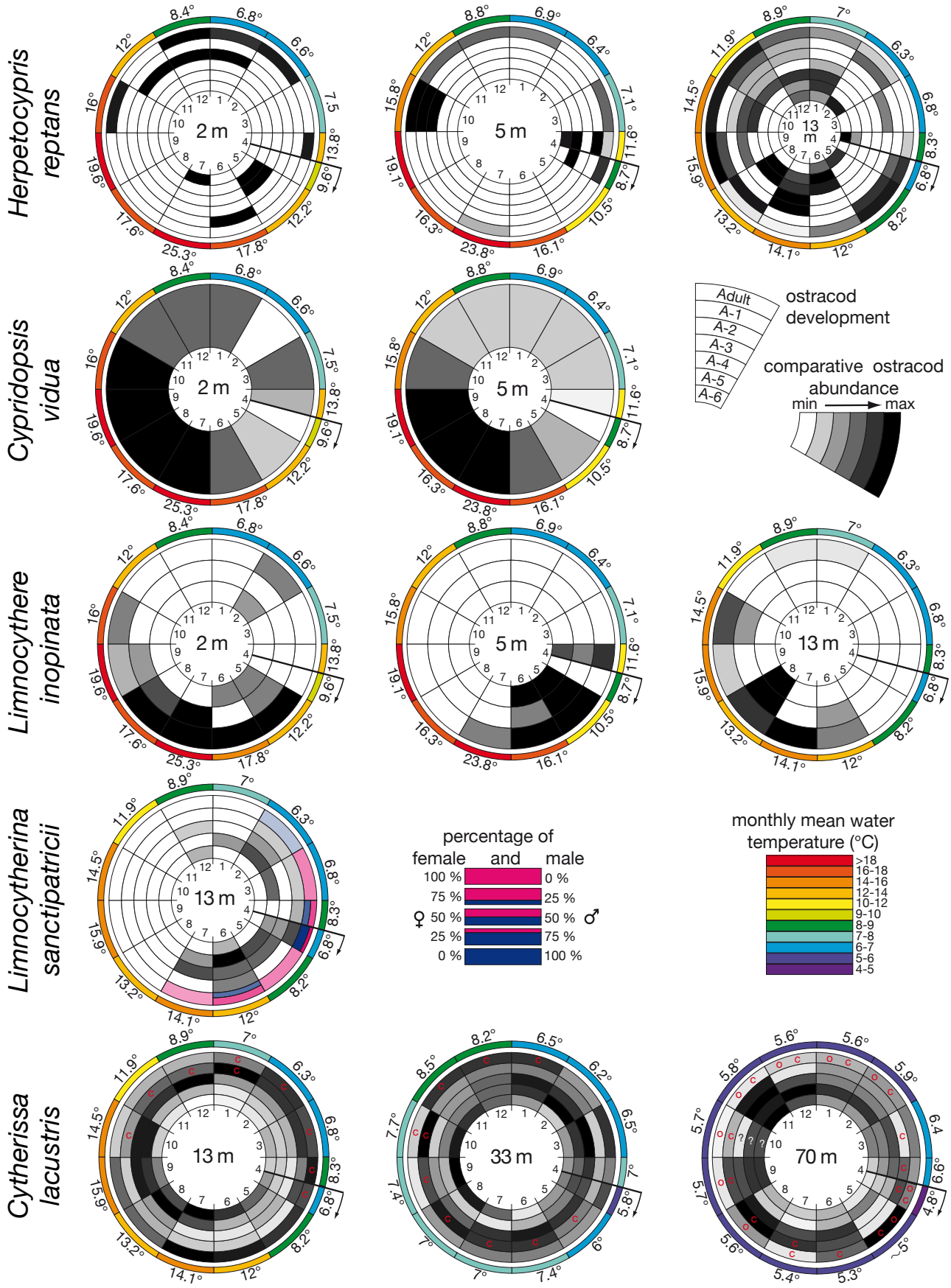


FIGURE 3.9
Life-cycle of the species belonging to the Cyprididae Family and to the Cytheroidea Superfamily using SOWM. The red «C» symbolise period of moulting, the red «O» symbolise old specimens (see text).

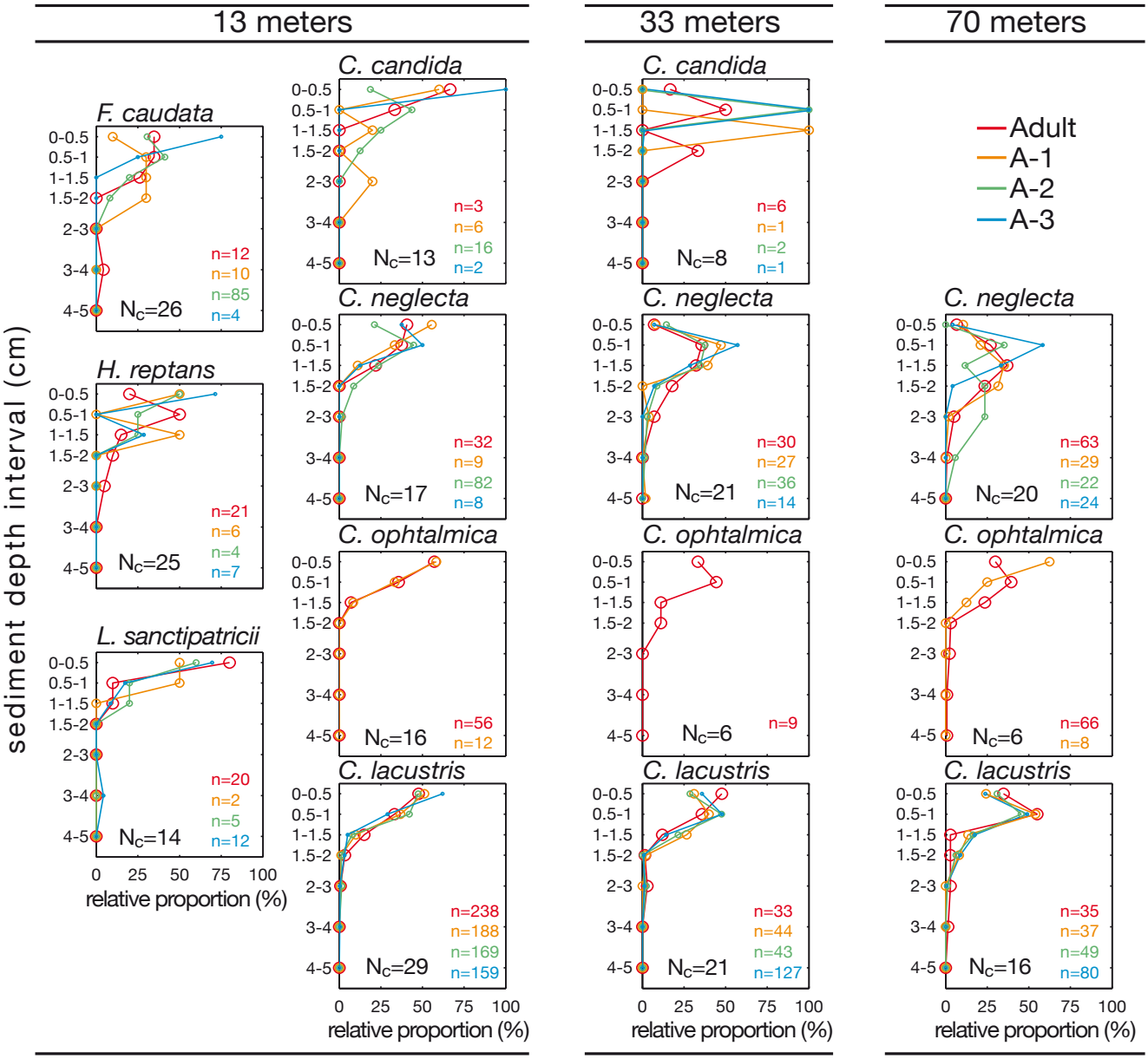


FIGURE 3.10
Ostracod sediment penetration depths of the most important species at 13, 33, and 70 meters water depths. «Nc» correspond to the number of cores, red «n» for the number of adult specimens, orange «n» for A-1, green «n» for A-2 and blue «n» for A-3. Penetration depths of A-4 specimens was identical to A-3 and are therefore not illustrated here.

3.5. Ostracod Sedimentation Penetration Depth

Geiger (1990b) observed that the distribution of individuals of *Cytherissa lacustris* in sediments is determined by the redox conditions and thus by oxygen concentrations in interstitial water. Most of the individuals were found in the uppermost layer (0-1 cm) where redox potential was high (> 275 mV). Corbari and co-authors (2004) confirmed that ostracod depth distribution in sediment was directly linked to oxygen concentration. They found that specimens of *Leptocythere castanea* and *Cyprideis torosa* adjust their tissue oxygenation by migrating through the O_2 gradient within sediments to where the P_{O2} of the interstitial water is between 3 to 5 kPa. Factors other than oxygen may influence ostracod distribution in sediments though. Ostracods can explore the sediments in search of nutrients as shown by the behaviour of *Cypridopsis vidua* (Roca and Danielopol, 1991). Burrowing is also a very efficient measure of protection against predators, as described for *C. lacustris* (Mbahinzireki et al., 1991). This species also avoids contaminated sediments (Danielopol, et al., 1990a). In addition, factors such as quality and texture of the substrate can restrain *C. lacustris* from burrowing and depth penetration also depends on the compactness of the sediment more than simply the grain size (Danielopol et al.,

1988). The depth of penetration clearly also depends on the development stage of the ostracods: younger juveniles generally remain in the well-oxygenated uppermost sediment layer, whereas, older juveniles and adults are able to dig deeper. Lower survival at low oxygen concentration and inferior number of sieve pores of juveniles of *C. lacustris* suggest that younger specimens need higher amounts of oxygen, explaining their relatively shallow microhabitat compared to adults (Geiger, 1990b).

In the method used for this study, the sediment cores have been sliced off from the collected column as they were retrieved. As the whole column is exposed to light, different temperature and pressure conditions and is also agitated by the handling, the ostracods within the sediment column may react in a protective way and dig deeper in order to find shelter or simply enter into a phase of inactivity. Even if great care was taken to handle the cores smoothly and rapidly, several minutes pass by before the sediment column is treated. A simple comparison between selected cores and cores that remained longer on board for measurements and water sampling indicates that ostracod penetration depth, especially those of adults, tends to increase slightly for cores that were sampled more slowly. This suggests that ostracods try to escape by burrowing into the sediment. Thus sediment penetration depth may be overestimated. Results illustrated here can, therefore, be interpreted as a relative distribution along sediment depth and/or the digging ability of the specimen. However, values observed in the present study are comparable to those of existing data (Danielopol et al., 1988; Griffiths and Martin, 1993; Corbari et al., 2004).

In general, most of the individuals are found in the first centimetre and ostracod penetration depth increases with water depth. This is, in part related to a grain size decrease of the sediment with increasing water depth. In addition, the water content of the sediment increases with depth and both of these factors lead to a softer sediment with increasing water depth (Table 3.3).

For most of the species, penetration depth increases with development (*C. neglecta*, *C. ophtalmica*, and *H. reptans*). For others, younger juveniles and adults prefer superficial microhabitats but intermediate juveniles are found slightly deeper (*C. candida* and *F. caudata*). For *C. lacustris*, even if adults are occasionally able to dig down to 3-4 cm, juveniles are generally found somewhat deeper than older specimens. For *L. sanctipatricii*, there is no difference between the different development stages. In terms of preferences, the data suggest that *C. candida* and *L. sanctipatricii* live in the superficial sediment, *F. caudata*, *C. ophtalmica*, *H. reptans*, and *C. lacustris* live a little deeper in the sediment, and *C. neglecta* prefers a deeper microhabitat. Surprising is the relatively large penetration depth of *C. ophtalmica*. This species is actually generally described as an epifaunal form and possesses well-developed natatory setae. An unusual infaunal microhabitat for *C. ophtalmica* was already observed in Loch Ness where the species was homogeneously distributed down to 5 cm within the sediment (Griffiths & Martin, 1993). It is not known if this habitat depth is permanent or rather related to a temporary search for food or shelter.

4. Conclusions

The ostracod fauna of the "Petit-Lac" is typical of a mid-latitude, deep, and large, mesotrophic lake: species and individual abundance is at a maximum in the littoral to sublittoral zones because of optimal oxygen and food conditions and habitat richness conditions, whereas lower species and individual abundance due to lower nutriment and oxygen availability are found in the profundal zones.

The species-specific distributions and individual abundances are controlled by a complex interconnection of factors. The most important are: water temperature, hydrological regime, sediment type and texture, food supply, and oxygen availability. The effects of competition and predation are more difficult to assess but can further restrict species distribution in non-optimal environments.

Microhabitat of the different species reflects their general ecological features: swimmer versus digger, food type, oxygen needs and anti-predation strategy. In the "Petit-Lac", the sediment penetration depth of a given species is mainly restricted by the texture ('softness') of the sediment. Besides, the ability to dig also depends on the development stage, with juveniles preferentially found higher up within the sediments.

Life-cycle of the different species in the littoral to sub-profundal zones (2 to 13 m depths) is clearly dictated by seasonal variations of water temperature. In the deepest part of the basin, where the environmental conditions remain stable, ostracod development is less or not cyclic at all. Slight development trends can be attributed to small seasonal variations of

nutrient supply from the epilimnion, optimal oxygen conditions after a winter overturn and a small increase in water temperature in autumn.

Species of the Candoninae Family are able to adapt their development to survive unfavourable conditions. A latent period in their development (‘diapause’) permits them to await the return of favourable conditions.

Because of the last two points, the life-cycle of a given species, and thus its moulting period can differ from one place to another. Knowledge of the ecology, especially of the life-cycle of the species is, therefore, important when ostracod species assemblages and/ or the geochemical compositions of the valves are used for environmental and palaeoenvironmental interpretations.

Chapter IV :

FACTORS CONTROLLING THE WATER ISOTOPIC COMPOSITION AND CHEMISTRY OF OSTRACOD HABITATS: CASE STUDY OF A WELL-OXYGENATED FRESHWATER SYSTEM, LAKE GENEVA, SWITZERLAND

1. Introduction

Ostracods are small microcrustaceans embedded into two low-Mg calcite valves. Like other crustaceans, ostracods grow by successive moulting (ecdysis). The carapace is cast and a new one is calcified within a few hours (Turpen and Angell, 1971) to a few days (Roca and Wansard, 1997). Most ostracods are benthic organisms that colonize almost all types of aquatic environments. In lakes, they occur from the littoral zones down to great depths. In addition, ostracod fossils are generally abundant and well-preserved in the sediment. Hence, their presence or absence or their relative abundance may already represent a valuable archive of past environmental conditions. In addition, trace element content of ostracod valves have proven useful for palaeoenvironmental reconstructions in marine, brackish, and freshwater environments (De Deckker et al., 1988; Engstrom and Nelson, 1991; Chivas et al., 1993; Dwyer et al., 1995, 2002; Wansard, 1996; Ricketts et al., 2001; Anadón et al., 2002; Palacios-Fest et al., 2002; Yu et al., 2002; Janz and Vennemann, 2005; Tütken and Vennemann, 2006). In continental areas, oxygen isotope compositions of ostracods were successfully employed to reconstruct past air temperatures (e.g. Lister, 1988; Schwalb et al., 1994, von Grafenstein et al, 1999a). The use of ostracods as palaeoenvironmental proxy necessitates that two important conditions are fulfilled: the environmental parameters (e.g. water Mg/Ca, Sr/Ca, $\delta^{18}O$, temperature, etc…) must be recorded in the valves and we must be able to interpret the geological archives in term of past environmental conditions (e.g. air temperature, precipitation/evaporation, etc…). Using laboratory experiments or 'natural environment cultures', several studies succeeded in calibrating the incorporation of trace elements and stable isotopes in ostracod shells (Chivas et al., 1983, 1986, 2002; Dwyer et al., 1995; Engstrom and Nelson, 1991; Xia et al., 1997; De Deckker et al., 1999; von Grafenstein et al., 1999b; Palacios-Fest and Dettman, 2001; Wansard and Mezquita, 2001; Keatings et al., 2002; Cronin et al., 2005; Kondo et al., 2005). The monitoring of environmental parameters over long periods and the observation of modern analogues permitted the formulation of general rules relating geological archives to environmental conditions (e.g., Rozanski et al., 1993). This knowledge forms the basis of the final interpretation.

However, no studies have so far examined in detail the variations of the geochemical composition of water in the precise macro- and micro-habitat of ostracods. As it is actually the ambient water surrounding the ostracod during moulting that is recorded in the shells, it is essential to understand the link between the ambient water and the general environment. The present study hence investigates the geochemistry of ostracod macro- and micro-habitats and links the variations observed to larger environmental phenomena. This permits a determination of which environmental factors are potentially recorded in ostracod shells. For a complete evaluation, though, ostracod autoecology has to be included in the interpretation of the results.

2. Results and Discussion

To discuss the different factors that influence the ostracod in their habitats and indirectly control their valve geochemistry, variations of the different environmental parameters (e.g., water Mg/Ca, Sr/Ca, $\delta^{18}O$, $\delta^{13}C_{DIC}$, temperature, etc…) are briefly described below. Where necessary, simple models are given to explain the measured variations and to examine the relative importance of the different external factors on the geochemistry of the water. In general, the geochemical composition of water in Lake Geneva is very stable. Nevertheless, seasonal variations are observed in the epilimnion. Besides, modifications of the water composition occur in the sediment interstitial pores.

Three types of environments are examined here: 1) the water column, corresponding to the zone where the basin is the deepest; 2) the bottom water,

corresponding to the water just above the sediment in the five sampling sites; and 3) the interstitial pore water, corresponding to the water extracted from the top five centimetres of sediment. For reasons of convenience, the three types of water are discussed independently. Based on the results of the three types of water, the potential incorporation of the different environmental factors in ostracod shells is evaluated.

2.1. Geochemical Composition of Water

2.1.1 Column water

A mass balance for the oxygen isotope composition of Lake Geneva demonstrates that lake $\delta^{18}O_{H2O}$ value results from the mixing of inflowing rivers and effect of evaporation (Favre and Piffarerio, 2006; Vennemann et al., *in prep.*). The same study showed that $\delta^{13}C_{DIC}$ value of the lake water is mainly controlled by $\delta^{13}C_{DIC}$ values of the major inflowing rivers, equilibration with the atmosphere, photosynthesis, and respiration.

Two previous unpublished master theses completed at the Stable Isotope Laboratory of the University of Lausanne investigated physico-chemical and isotopic compositions of the water column from the "Grand-Lac" and from the "Petit-Lac" (Decrouy, 2004; Favre and Piffarerio, 2006). Results of these studies allow us to examine the seasonal variations within the lake as well as the differences between the two sub-basins. Emplacement of the two studied sites (*PL* and *GL*) are shown in Figure 2.1 A and B.

$\delta^{18}O_{H2O}$ values in the hypolimnion of the "Grand-Lac" has been very stable over the last 40 years, ranging between –12.3 and –12.5 ‰ VSMOW. Slight enrichments in ^{18}O due to evaporation of superficial water during summer were observed in the epilimnion in several specific places (Fontes and Gonfiantini, 1970; Lemeille, 1980; Chaix et al., 1982; Decrouy, 2004; Favre and Piffarerio, 2006).

Typical winter and summer column water $\delta^{13}C_{DIC}$ values measured in the "Grand-Lac" (*GL*) and the "Petit-Lac" (*PL*) are illustrated in Figure 4.1. The observed seasonal variations are typical for large mesotrophic lakes. During winter, $\delta^{13}C_{DIC}$ values are constant for the whole water column with values ranging from –7 to –8 ‰ VPDB. As water temperature increases, the preferential uptake of ^{12}C by phytoplankton during photosynthesis leads to a sharp increase of the $\delta^{13}C_{DIC}$ values in the epilimnion where $\delta^{13}C_{DIC}$ values reach –5 to –1 ‰ VPDB. Although strong seasonal variations are observed in the epilimnion, $\delta^{13}C_{DIC}$ values in the hypolimnion remain mostly constant throughout the

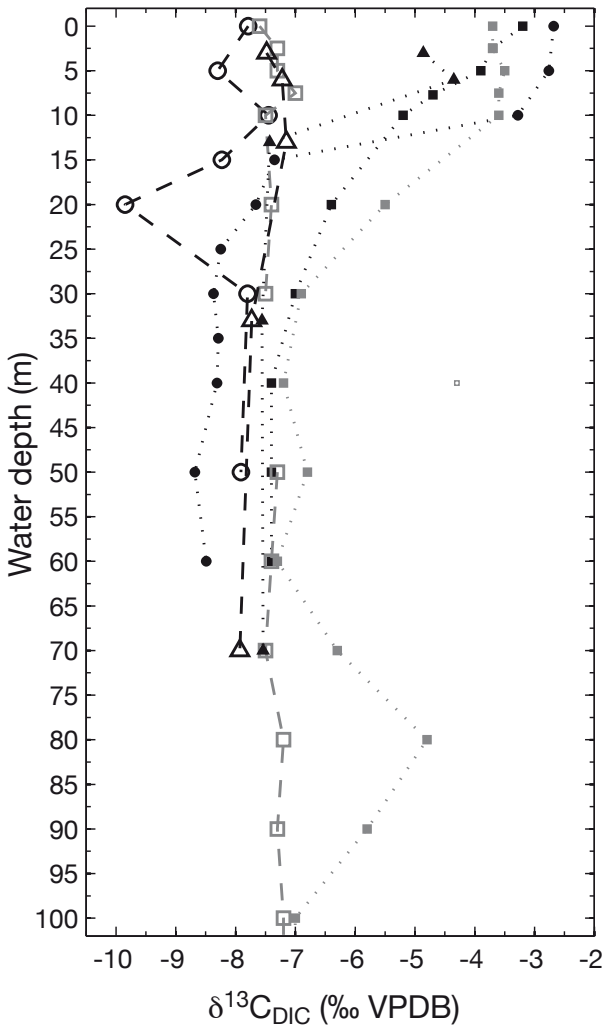


FIGURE 4.1
Carbon isotope compositions of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) of selected column water profiles measured in the "Grand-Lac" (grey squares) and in the "Petit-Lac" (black circles), and in the five studied sites (black triangles). Markers for winter values are larger, unfilled and joined up with dashed lines, markers for summer values are smaller, filled in and joined up with dotted lines.

year; and this even during highly productive periods. Generally, organic matter is remineralised as it sinks in the hypolimnion. This releases the ^{12}C entrapped in organic matter and leads to a decrease of $\delta^{13}C_{DIC}$ values under the thermocline (Kroopnick et al., 1972; McKenzie, 1985; Quay et al., 1986; Herczeg, 1987; Miyajima et al., 1995). Release of ^{12}C in the hypolimnion certainly occurs in Lake Geneva. Still, the effect remains insignificant on deep-water $\delta^{13}C_{DIC}$ values because of the extremely large size of the hypolimnion DIC pool of the "Grand-Lac". Hence, the DIC pool of the Petit-Lac is much smaller but water residence time in this sub-basin is only of a few months. The deep water in the Petit-Lac is therefore continuously regenerated by hypolimnion water from the "Grand-Lac" and ^{12}C can not accumulate. Note

TABLE 4.1
Monthly physico-chemical and isotopic values determined for the five studied sites.

site	sampling	date	temperature (°C)	pH	[DIC] (mmol/l)	$\delta^{13}C_{DIC}$ (‰ VPDB)	$\delta^{18}O_{H2O}$ (‰ VSMOW)	Ca^{2+} (mg/l)	Mg^{2+} (mg/l)	Sr^{2+} (mg/l)
2 m	A	04.07.06	7.2	N.D.	1.51	-8.9	-12.0	50.0	6.28	0.428
	C	04.25.06	19.9	8.9	1.23	-4.9	-12.5	40.1	6.11	0.451
	E	05.24.06	11.3	8.2	1.13	-7.7	-12.4	45.0	6.03	0.465
	G	06.19.06	20.0	8.8	1.07	-5.6	-12.4	42.6	5.99	0.455
	I	07.25.06	26.8	8.4	1.22	-4.0	-11.9	34.9	5.91	0.439
	K	08.31.06	15.0	7.9	1.04	-6.4	-12.4	42.1	5.93	0.447
	M	10.04.06	13.8	8.2	1.39	-6.7	-12.4	40.1	5.47	0.448
	O	10.25.06	14.3	8.1	N.D.	-6.9	-12.3	40.9	5.62	0.446
	Q	11.28.06	11.2	8.4	0.97	-5.9	-12.2	42.6	5.97	0.462
	S	01.09.07	7.2	8.0	1.35	-7.5	-12.2	43.2	5.60	0.468
	U	02.16.07	6.1	8.1	1.44	-8.3	-12.0	45.1	5.50	0.441
	W	03.12.07	7.2	8.1	1.67	-7.0	-12.1	48.4	6.32	0.471
	Y	04.10.07	11.7	8.5	1.27	-6.4	-12.1	43.9	5.76	0.473
	aa	05.01.07	17.1	8.5	1.32	-6.1	-12.1	44.5	6.23	0.470
5 m	A	04.07.06	6.5	N.D.	1.38	-7.6	-12.1	46.9	6.29	0.465
	C	04.25.06	14.4	8.9	1.06	-4.6	-12.4	40.6	5.93	0.450
	E	05.24.06	10.9	8.8	0.93	-7.3	-12.4	46.9	6.22	0.470
	G	06.19.06	17.9	8.7	1.12	-6.1	-12.4	45.5	6.47	0.464
	I	07.25.06	25.7	8.2	1.03	-5.3	-11.9	36.5	5.87	0.447
	K	08.31.06	15.2	8.3	1.00	-6.3	-12.4	38.0	6.20	0.452
	M	10.04.06	12.6	8.1	1.20	-7.1	-12.4	43.3	5.87	0.467
	O	10.25.06	13.7	7.8	N.D.	-7.7	-12.6	40.3	5.24	0.441
	Q	11.28.06	11.1	8.5	0.96	-6.0	-12.2	43.7	6.10	0.461
	S	01.09.07	7.2	8.1	1.25	-7.2	-12.2	47.1	6.40	0.481
	U	02.16.07	6.1	8.1	1.63	-9.3	-11.6	49.3	5.53	0.374
	W	03.12.07	7.1	8.2	1.54	-6.6	-12.2	43.8	5.65	0.470
	Y	04.10.07	10.0	8.6	1.32	-6.2	-12.2	45.4	6.05	0.414
	aa	05.01.07	16.6	8.7	1.42	-6.1	-12.1	48.0	6.51	0.454
13 m	A	04.07.06	5.9	N.D.	1.29	-7.3	-12.5	42.8	5.45	0.422
	B	04.19.06	6.6	8.8	1.19	-7.4	-12.5	46.0	5.92	0.464
	D	05.10.06	6.5	8.3	1.20	-8.2	-12.5	48.0	6.13	0.418
	F	06.12.06	12.0	8.3	1.05	-7.0	-12.4	44.9	5.88	0.422
	H	07.11.06	12.6	8.0	1.48	-7.2	-12.4	45.8	5.78	0.418
	J	08.16.06	19.0	8.1	0.90	-5.4	-12.3	38.9	5.72	0.413
	L	09.12.06	19.5	8.4	0.92	-5.3	-12.3	39.8	5.85	0.342
	N	10.10.06	15.3	8.0	1.15	-6.1	-12.4	42.3	5.82	0.393
	P	11.15.06	11.7	8.0	1.52	-6.5	-12.3	40.6	5.12	0.440
	R	12.12.06	9.1	8.3	1.18	-7.2	-12.2	43.7	5.21	0.474
	T	01.16.07	6.8	8.1	1.37	-7.3	-12.2	44.2	5.46	0.474
	V	02.20.07	6.4	8.2	1.32	-7.1	-12.2	45.1	6.03	0.475
	X	03.27.07	6.6	8.2	1.24	-7.1	-12.2	39.1	5.09	0.414
	Z	04.25.07	8.3	8.3	1.36	-7.1	-12.3	43.1	5.56	0.472
33 m	A	04.07.06	5.9	N.D.	1.53	-7.5	-12.5	45.9	6.11	0.485
	C	04.25.06	6.2	8.3	1.49	-7.6	-12.5	45.4	6.05	0.461
	E	05.24.06	6.4	8.4	1.19	-8.3	-12.4	48.7	5.92	0.481
	G	06.19.06	7.6	8.0	1.46	-7.8	-12.4	44.9	5.88	0.489
	I	07.25.06	6.3	8.2	1.23	-8.9	-12.3	46.5	6.11	0.490
	K	08.31.06	8.3	7.4	1.15	-8.1	-12.50	45.8	6.03	0.487
	M	10.04.06	6.6	7.7	1.27	-7.9	-12.3	48.2	6.31	0.504
	O	10.25.06	7.2	7.8	N.D.	-8.2	-12.4	47.4	6.22	0.504
	Q	11.28.06	8.3	8.0	1.25	-7.8	-12.3	43.3	5.63	0.475
	S	01.09.07	6.5	8.0	1.24	-7.7	-12.3	48.1	6.39	0.503
	U	02.15.07	6.0	8.1	1.37	-7.2	-12.2	45.9	6.08	0.486
	W	03.12.07	6.6	8.1	1.59	-6.8	-12.2	43.5	5.62	0.462
	Y	04.10.07	7.1	8.2	1.29	-7.0	-12.3	44.7	5.85	0.485
	aa	05.01.07	7.2	8.3	1.46	-7.4	-12.2	47.7	6.28	0.489
70 m	A	04.07.06	4.5	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.	N.D.
	B	04.19.06	5.0	8.5	1.21	-7.5	-12.6	48.7	6.50	0.391
	D	05.10.06	5.0	8.3	1.03	-8.3	-12.4	47.0	6.03	0.382
	F	06.12.06	5.0	8.3	1.27	-8.0	-12.6	46.0	5.93	0.383
	H	07.11.06	5.4	8.1	1.48	-7.7	-12.3	47.3	6.37	0.387
	J	08.16.06	5.5	7.7	1.19	-7.9	-12.4	46.1	5.99	0.428
	L	09.12.06	5.7	7.6	1.07	-8.1	-12.5	46.4	6.05	0.476
	N	10.10.06	5.6	8.0	1.33	-8.0	-12.3	48.6	6.35	0.388
	P	11.15.06	5.8	8.2	1.33	-8.0	-12.3	46.2	5.95	0.379
	R	12.12.06	5.5	8.2	1.35	-7.9	-12.3	46.3	5.97	0.380
	T	01.16.07	5.5	7.9	1.34	-8.1	-12.2	46.6	6.05	0.463
	V	02.20.07	5.9	7.8	1.44	-7.9	-12.3	47.0	6.08	0.365
	X	03.27.07	6.6	8.1	1.44	-7.4	-12.2	46.0	5.95	0.363
	Z	04.25.07	6.7	8.1	1.40	-7.5	-12.3	43.2	5.55	0.352

that the negative and positive shifts at 20, 40, and 80 m depths on Figure 4.1 are interpreted as inflowing water masses from major streams (Rhône, Dranse, and Versoix rivers).

2.1.2. Bottom water

Monthly temperatures, pH, [DIC], $\delta^{13}C_{DIC}$, $\delta^{18}O_{H2O}$, Ca^{2+}, Mg^{2+}, and Sr^{2+} measured at the five studied sites are presented in Table 4.1 and illustrated in Figure 4.2. Typical winter and summer $\delta^{13}C_{DIC}$ values for bottom water are also displayed on Figure 4.1 (triangles) to allow for comparison with the column water. One can see that bottom water values are nearly identical to the ones for column water. Other studies showed that bottom water geochemistry often differs passably from that of the column water. Generally, degradation of organic matter taking place in the sediment diffuses ^{12}C enriched carbon dioxide to the bottom water leading to relatively low $\delta^{13}C_{DIC}$ values of bottom water

(Miyajima et al., 1995). Sometimes, methanogenesis takes place in the sediment and releases enriched carbon dioxide into the bottom water leading to an increase of $\delta^{13}C_{DIC}$ values of bottom water (Hesslein, 1980; Quay et al., 1986; Herczeg, 1987). As bottom and column water $\delta^{13}C_{DIC}$ values are identical in the Petit-Lac, influence of pore water on bottom water must be insignificant. This may be due to low diffusion fluxes of DIC from sediment to bottom water. This may also results from constant mixing of bottom water because of the strong currents sweeping across the bottom of the basin during windy periods (see below and Ulmann et al. 2003).

During the sampling period, water temperature ranges from 2.1 to 28°C (Fig. 4.2). The 'continuous' water temperature record reflects faithfully the meteorological condition experienced throughout the year. Lowest values were measured during the fairly cold winter 2005-2006. Summer 2006 was characterised by an unusual warm month of July and an abrupt cooling at the beginning of August. Autumn 2006 was abnormally warm and winter 2006-2007 exceptionally mild. Early spring 2007 was also exceptionally warm with record air temperatures for the month of April. A comparison with meteorological data from "MeteoSwiss " (MeteoSwiss, pers. comm.) reveals that water temperature at 2, 5 and, with a certain lag at 13 m, follows directly the air temperature. Besides, water temperature at 33 and 70 m increases continuously during this unusual warm year and is only slightly lowered during winter 2006-2007. Shorter term and more abrupt variations overprint the general trend controlled by air temperature and/ or solar radiation. Rapid and drastic warming at 13 and 33 m water depths as well as rapid cooling at 2, 5, and 13 m are synchronous with a prolonged period of strong winds. In the region of the "Petit-Lac", wind follows a NE-SW trending long axis of the basin. Due to the bottleneck morphology of the basin of the "Petit-Lac" and parallel wind direction, the effect of the wind on the superficial water is amplified and strong deep currents are established to accommodate the displacement of superficial water (Ulmann et al., 2003). During SE wind events, superficial water is pushed to the NE leading to an upwelling of cold deep water at the SE end of the basin and along both shores. During these periods, water temperature at 33 m remains constant since this station lies under the thermocline, whereas water temperature at 2, 5, and 13 m decreases sharply. When the wind is blowing from the NE, superficial water is pushed to the SW end of the basin and to the shore of the basin causing a downwelling of superficial water along the slopes. During these episodes, warm water penetrates the hypolimnion and water temperature at 13 and 33 m increases sharply but remains constant at 2 and 5 m. When wind finally stops, return to preceding equilibrium is very rapid. These results illustrate nicely the extremely dynamic hydrology of the basin as well as the importance of water mixing and fast recycling of bottom water.

The 'punctual' water temperature record together with pH, $\delta^{18}O_{H2O}$, [DIC], $\delta^{13}C_{DIC}$, Mg/Ca, and calcite saturation index are displayed on the lower part of Figure 4.2. Values for 'punctual' temperature record equals the values of the 'continuous' record for the same date and time, but differ significantly from average temperatures calculated from the 'continuous' record. As the 'punctual' water temperature values correspond to the specific conditions during the sampling, these values are used for comparison with other measured parameters.

The pH of Lake Geneva bottom water ranges between 7.4 and 9.0. Values at the five stations follow the same general trend with maximal values in spring, followed by a gradual decrease of the values in August and minimal, relatively constant, values in autumn and winter. A closer inspection shows that epilimnion bottom water has higher pH values than hypolimnion bottom water during spring and summer. Lower values are reached in the deepest sites (33 and 70 m) in summer and these values increase afterward slightly during autumn. The difference of pH between epilimnion and hypolimnion decreases in autumn and, when the water column is finally mixed in winter, pH values of all sites are equal. Generally, an increase of pH in epilimnion during spring and summer is linked to removal of CO_2 during photosynthesis. This would be expected to be followed by a rise of $\delta^{13}C_{DIC}$ values. As dead algae sink, remineralisation of the organic tissue releases CO_2 in the hypolimnion, leading to a slight decrease of pH in hypolimnion and a decrease of $\delta^{13}C_{DIC}$ values (e.g. Quay et al, 1986). Since pH evolves concomitantly in the epilimnion and hypolimnion and is not consistent with $\delta^{13}C_{DIC}$ record, the present dataset deviates from this general model. It is thought that the most important reason for this is that the water investigated here consists of bottom water and not column water. The difference between both environments is that in bottom water, organic matter produced during photosynthesis is not removed from the system by sinking in the hypolimnion but is remineralised in place. Thus, there is a complex interaction between photosynthesis and organic matter degradation. Moreover, many other factors than CO_2 release and uptake can affect pH in lake water. Hence no satisfactory model could be given for pH variation.

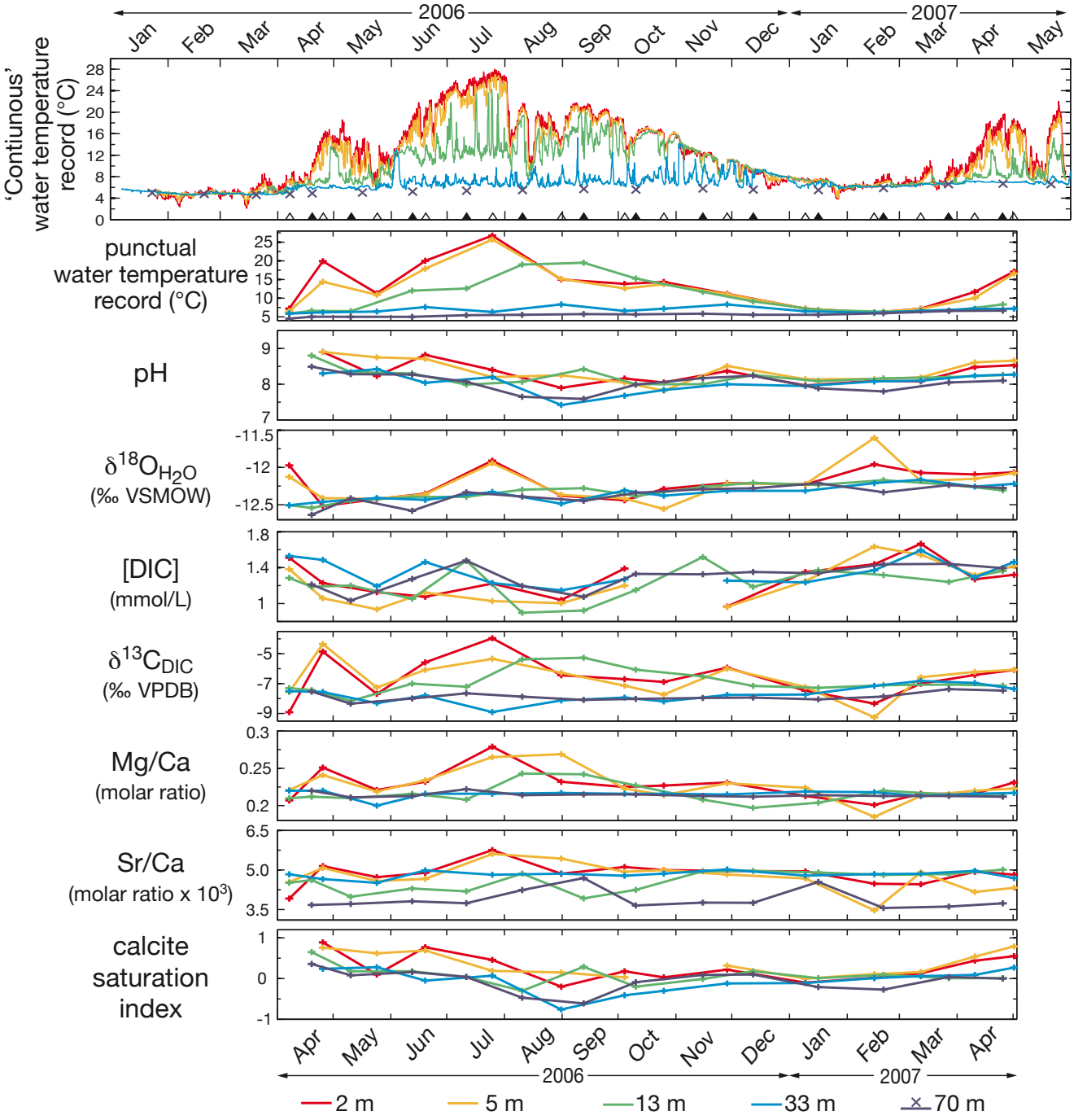


FIGURE 4.2
Monthly physico-chemical and isotopic values determined for bottom water at the five studied sites.

Concerning the oxygen isotopic composition of water, one can see on Figure 4.2 that $\delta^{18}O_{H2O}$ values increase gradually from about –12.5 to –12.3 ‰ VSMOW during the sampling year. These values are in the range of the different punctual measurements made during the last 50 years (see section 3.1.1). This slight global increase may be attributed to higher values of inflowing water of local rivers in the "Petit-Lac" due to global warming reinforced by the unusual warmness of the studied period. This signal may be only local and may not have been observed in the "Grand-Lac" where the water pool is much larger with a corresponding smaller variation of oxygen isotopic composition. The peaks observed in April and February at 2 and 5 m were interpreted as water contributions of nearby streams that present all year round high $\delta^{18}O_{H2O}$ values (Decrouy, 2004; Favre & Piffarerio, 2006). The peaks measured at the end of July in the littoral zones are, as for them, correlated with the highest water temperature recorded during the year and were interpreted as ensuing from evaporation of superficial water.

In Figure 4.2, $\delta^{13}C_{DIC}$ values are uniform at the beginning of the sampling period for the five stations and represent equilibrium after winter

mixing (–7.5 ‰VPDB). As water temperature increases in superficial water, photosynthesis sets in and values reach –6 to –4 ‰ VPDB at 2 and 5 m. Water temperature at 13 m increases slower and photosynthesis is, at this depth, delayed in time. Bottom water of the hypolimnion (33 and 70 m) is slightly enriched in ^{12}C due to remineralisation of sinking organic matter. When water temperature decreases and water begins to mix in autumn, the $\delta^{13}C_{DIC}$ values of epilimnion bottom water decrease, whereas values of hypolimnion bottom water increase. This goes on until total homogenisation of water column and return to winter equilibrium values (–7.5 ‰ VPDB).

As can be seen from graphs on Figure 4.2, 'punctual temperature', $\delta^{13}C_{DIC}$, Mg/Ca ratios and Sr/Ca ratios vary concomitantly in the littoral zone, whereas values remain relatively stable in the deepest stations, i.e. at 33 and 70 m. The linear positive relationships between these parameters are illustrated in Figure 4.3 A, B, and C. The relationship between $\delta^{13}C_{DIC}$ and water temperature implies that the factor limiting productivity in the three sites is water temperature and/or solar radiation rather than nutriment availability. A study made on a sediment short core from the "Petit-Lac" showed that sediment opal content increases in parallel with air temperature and was not linked to water nutriment content. This confirms that nutrient may not be the limiting factor for algal production in this basin (Jaccard et al., 2009). This phenomenon is rather unusual. Large amounts of deep-water rich in nutrient inflowing from the "Grand-Lac" into the "Petit-Lac" may explain this particularity. Running waters inflowing the littoral zones may also continuously provide nutriments to the studied sites. Another point of interest is that best correlations between these factors were found with the 'punctual' water temperatures and not daily or weekly averages calculated from the 'continuous' water temperature record. This suggests that variations of $\delta^{13}C_{DIC}$ values are very dynamic and that $\delta^{13}C_{DIC}$ values are very sensible to small environmental changes. A closer inspection of the variations of the Ca^{2+}, Mg^{2+}, and Sr^{2+} contents (Table 4.11) reveals that Mg^{2+} and Sr^{2+} are conservative whereas Ca^{2+} decreases during warm months. These observations were attributed to calcite precipitation. Macroalgae and macrophytes, both very frequent in the littoral zones of the "Petit-Lac", are known to precipitate calcite during active photosynthesis (Hutchinson, 1957; Wetzel, 1960). Phytoplankton is also known to induce calcite precipitation during photosynthesis (Stabel, 1986). The fact that $\delta^{13}C_{DIC}$ values (Fig. 4.3 A) and Mg/Ca and Sr/Ca ratios (Fig. 4.3 B and C) are correlated with water temperature suggests that photosynthetic production rate controls calcite precipitation. The

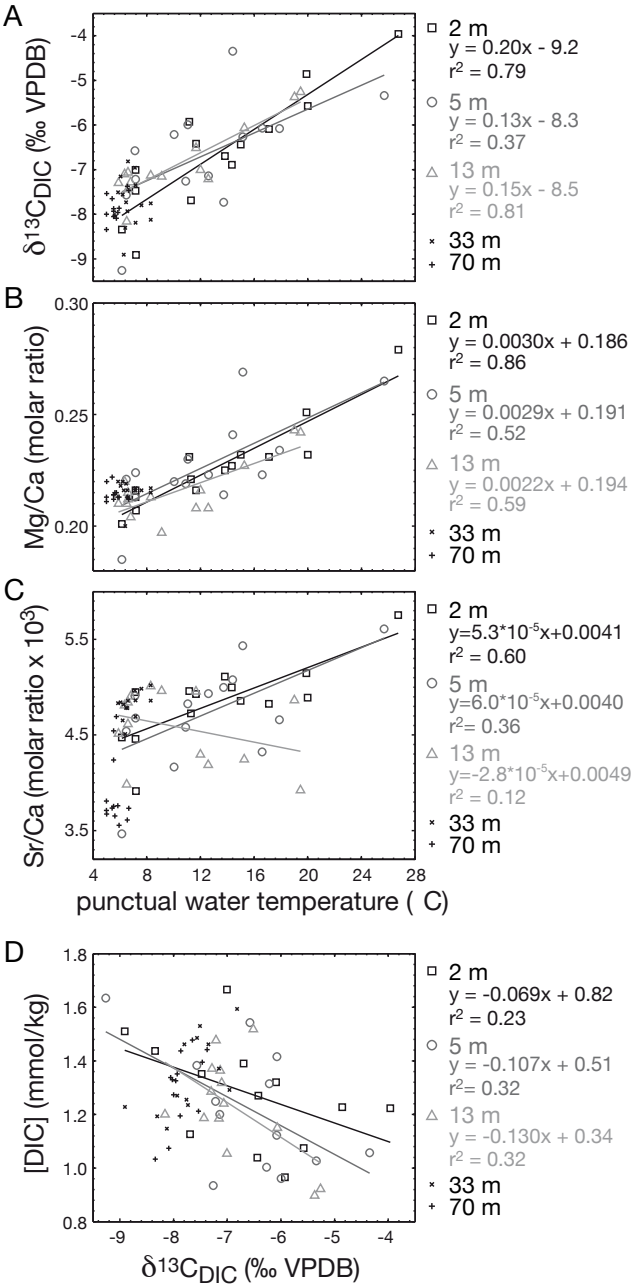


FIGURE 4.3
Linear correlations between selected environmental parameters: carbon isotope composition of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) versus water temperature (A), Mg/Ca ratios of water versus water temperature (B), Sr/Ca ratios of water versus water temperature (C), and dissolved inorganic carbon concentration ([DIC]) versus $\delta^{13}C_{DIC}$.

non-coherence between the Mg/Ca (as well as Sr/Ca) record of calcite precipitation and the calculated calcite saturation index is surprising. Calcite saturation index reflects mainly the variation of the pH, but in this case, both are non-coherent with photosynthetic productivity. Calcite precipitation localised just around macroalgae and macrophytes may explain this apparent discrepancy.

DIC concentrations show a slight decrease during warm period (Fig. 4.2). On Figure 4.3 D, a minor

TABLE 4.2
Sediment characteristics at 13, 33, and 70 m water depth.

site	13 m			33 m			70 m		
sediment characteristics	silty-sand; allochtonous micrite, bioclasts and detricitic carbonnates, colonies of zebra mussels			clayed-silt, very fine fluffy texture			clayed-silt, very fine fluffy texture		
water content	86 wt%	± 6	n=17	93 wt%	± 3	n=20	95 wt%	± 2	n=20
% TOC (dried weigth)	1.4 wt%	± 0.4	n=17	2.9 wt%	± 0.3	n=20	3.3 wt%	± 0.4	n=20
$\delta^{13}C_{OM}$ (‰ VPDB)	-26.70	± 0.57	n=17	-27.23	± 0.42	n=20	-27.94	± 0.21	n=20
C/N (molar ratio)	7.8	± 1.0	n=10	7.1	± 0.6	n=10	7.4	± 0.6	n=10
% CaCO3 (dried weigth)	62 wt%	± 6	n=17	45 wt%	± 4	n=20	44 wt%	± 5	n=20
$\delta^{13}C_{CaCO3}$ (‰ VPDB)	-1.23	± 0.43	n=17	-2.86	± 0.17	n=20	-2.64	± 0.11	n=20
$\delta^{18}O_{CaCO3}$ (‰ VPDB)	-10.95	± 031	n=17	-12.06	± 0.22	n=20	-11.82	± 0.22	n=20

inverse correlation is found between [DIC] and $\delta^{13}C_{DIC}$ in shallow water (Fig. 4.3 D). This shows that during photosynthesis, phytoplankton takes up carbon from the DIC pool whereas remineralisation of organic matter releases carbon in DIC pool in winter.

To summerize, the geochemical composition of bottom water appears to be largely controlled by seasonal variations is the photosynthesis-respiration cycle. Variations of [DIC], $\delta^{13}C_{DIC}$, and Mg/Ca and Sr/Ca ratios reflect the balance between the two terms of the couple. pH behaviour is more complex and may be strongly affected by other components. Besides, the whole system is very dynamic and water geochemistry can change rapidly as a function of the environmental conditions.

2.1.3. Sediment Pore Water

Sediment characteristics at 13, 33, and 70 m water depths are displayed in Table 4.2. Sediments at 13 m consist of silty-sand, with 62 wt% (dried weight) of carbonate, 1.4 wt% (dried weight) of organic carbon (TOC), and silicates (mainly sand, clay, and silt). At 33 and 70 m, sediments are made up of clayed-silt, with lower proportions of carbonates (~ 45 wt%, dried weight) but higher proportions of organic mater (TOC ≈ 3 wt%, dried weight), and silicates (mainly clay and silt fraction). Water content is high at all depth (86 to 95 wt%). Stable isotope composition of bulk sedimentary carbonates ($\delta^{13}C_{CaCO3}$ and $\delta^{18}O_{CaCO3}$) approximately equals –2 and –11 ‰ VPDB for carbon and oxygen, respectively. Mass balance calculation based on the isotopic composition of detrital carbonates ($\delta^{13}C_{CaCO3}$ ≈ –2 to +3 ‰ VPDB; $\delta^{18}O_{CaCO3}$ ≈ –7 to –3 ‰ VPDB) and expected isotopic composition of authigenic calcite ($\delta^{13}C_{CaCO3}$ ≈ –3 ‰ VPDB; $\delta^{18}O_{CaCO3}$ ≈ –14.5 ‰ VPDB) indicates that carbonates fraction at 13 m water depth contain ~ 50 wt% detrital carbonates and ~ 50 wt% of authigenic calcite, whereas carbonates fraction at 33 and 70 m contain ~ 40 wt% of terrestrial carbonates and ~ 60 wt% of authigenic calcite. Organic matter contained in the sediment has a carbon isotope composition of approximately –27 ‰ VPDB and a C/N ratio of approximately 7.5 suggesting that it is produced by freshwater algae (Meyers, 1994). Sedimentary organic matter represents, therefore, the authigenic primary productivity.

Tables 4.3 and 4.4 present the Ca^{2+}, [DIC], and $\delta^{13}C_{DIC}$ of interstitial water for sites at 13, 33, and 70 m water depth. These results are illustrated graphically in Figure 4.4.

At the three sites, pH decreases slightly beneath the sediment-water interface and increases afterwards gradually with sediment depth. Variability of the microenvironments can be assessed by the importance of the standard deviation (1-sigma) represented by the horizontal bars on the graph and in Tables 4.3 and 4.4. The variability is relatively low in the sediment at 13 m with standard deviations equal to ± 0.2 to ± 0.4, but is higher in deeper sites with maximal variability of ± 0.65.

Calcium concentration in pore water is approximately 10 mg/l higher than in overlying (supernatant) water. Ca^{2+} profiles show slight enrichment under the sediment-water interface. Location of the increase corresponds to the sediment depth where the pH values are the lowest.

The carbon isotope composition of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) of pore water is clearly depleted in ^{13}C

in comparison with supernatant water. $\delta^{13}C_{DIC}$ values range between –6.1 to –14.7 ‰ VPDB and show, at first view, a logarithmic decrease with depth. A closer inspection reveals that, in the site at 70 m water depth, $\delta^{13}C_{DIC}$ values increase again to approximately –10 ‰ VPDB between 3 and 5 cm sediment depth.

In addition, the dissolved inorganic carbon concentration ([DIC]) increases gradually with depth: values range from 1.31 to 2.72 mmol/kg at 13 and 33 m; whereas the rise is higher at 70 m where [DIC] values attain 4.05 mmol/kg.

The calcite saturation index is mainly parallel to the pH trend. Pore water is barely saturated in the first centimetre of sediment but gets oversaturated within the sediment.

It is well known that microbial activity is important in modern sediments. The complex microbial activity results in a very strong interaction between sediment and pore water (e.g. Konhauser, 2007). The decrease of $\delta^{13}C_{DIC}$ values together with increase of [DIC] values and slight decrease of pH beneath sediment-water interface was interpreted as resulting from remineralisation of organic matter under aerobic condition. Once oxygen has been removed, remineralisation of organic matter can occur via respiration coupled with nitrate and sulphate reduction. These reactions typically lead to an increase in alkalinity and a rise of pH. Besides, the observed increase of $\delta^{13}C_{DIC}$ values within deep sediments at 70 m was linked to methanogenesis. Finally, the increase observed for Ca^{2+} can by explained by carbonate dissolution. Because calculated calcite saturation index indicates that calcite is saturated to oversaturated in pore water, dissolution of carbonate is at first view unexpected. As discussed above, large variations of calcite saturation among different microenvironments, such as small pockets of sediment where remineralisation of organic matter rate is high, may explain this apparent discrepancy.

To determine the different sources of pore water DIC, the graphical method presented by Hu and Burdige (2007) was followed. These authors showed that plots of $(\delta^{13}C_{DIC}) \bullet [DIC]$ versus [DIC] are generally linear and that the slope of such plots corresponds to the $\delta^{13}C_{DIC}$ value of the DIC being added to the pore waters ($\delta^{13}C_{add}$). Correlations between $(\delta^{13}C_{DIC}) \bullet [DIC]$ and [DIC] for the "Petit-Lac" are illustrated in Figure 4.5. For the site at 70 m, samples were classified into two groups; one with $\delta^{13}C_{DIC}$ values decreasing with depth, corresponding to sediment without methanogenesis and another, corresponding sediment with methanogenesis with $\delta^{13}C_{DIC}$ values increasing with depth. The relation between $(\delta^{13}C_{DIC}) \bullet [DIC]$ and [DIC] is inverse and linear with a significant correlation (r = –0.91 to –0.98). The carbon isotope compositions of added DIC ($\delta^{13}C_{add}$) in sediment without methanogenesis are fairly constant with values ranging from –15.1 ‰ VPDB at 13 m to –16.7 ‰ VPDB at 70 m. Carbon isotope composition of added DIC ($\delta^{13}C_{add}$) in sediment with methanogenesis is significantly higher with a calculated delta value of –9.8 ‰ VPDB.

TABLE 4.3
pH measured along sediment depth profiles at 13, 33, and 70 m water depths.

sediment depth (cm)	pH	std	pH	std	pH	std
	13 m		33 m		70 m	
B.W. (2 cm)	8.0	0.17	8.1	0.22	8.0	0.21
B.W. (0.5 cm)	8.0	0.18	8.1	0.22	8.0	0.18
0	7.9	0.20	8.0	0.22	7.9	0.23
0.5	7.9	0.17	7.9	0.18	7.8	0.26
1	8.0	0.12	7.9	0.18	8.0	0.29
1.5	8.1	0.13	8.0	0.20	8.1	0.44
2	8.2	0.18	8.1	0.32	8.3	0.48
2.5	8.2	0.23	8.2	0.35	8.4	0.53
3	8.3	0.28	8.3	0.39	8.4	0.57
3.5	8.4	0.30	8.5	0.42	8.5	0.58
4	8.5	0.28	8.5	0.42	8.5	0.58
4.5	8.7	0.22	8.5	0.42	8.5	0.59
5			8.5	0.42	8.5	0.59
5.5			8.5	0.43	8.5	0.64

Knowing the carbon isotopic composition of each term involved in the different reactions between sediments and pore water, a simple model can be developed to distinguish the different sources of DIC and their relative importance. Lack of data implied that the model has to be simplified. Each slice of sediment was, therefore, considered as being a closed system without any diffusion or advection processes. Furthermore, all DIC added to the carbon pool is considered to be derived from calcite dissolution and organic matter remineralisation; hence, calcite precipitation in the sediment was not taken into account.

Remineralisation of sedimentary organic matter by aerobic respiration produces metabolic CO_2. Approximating sediment organic matter as $<CH_2O>$, these processes can be expressed as:

$$<CH_2O> + O_2 \rightleftharpoons CO_2 + H_2O \qquad (4.1)$$

The carbon dioxide released from this reaction can react with sedimentary carbonates and cause their dissolution following the reaction:

$$CO_2 + CaCO_3 + H_2O \rightleftharpoons Ca^{2+} + 2\ HCO_3^- \qquad (4.2)$$

Reaction (1) and (2) can be summed as follows:

$$<CH_2O> + O_2 + CaCO_3 \rightleftharpoons Ca^{2+} + 2\ HCO_3^- \qquad (4.3)$$

TABLE 4.4
Geochemistry of sediment interstitial pore water at 13, 33, and 70 m water depths.

site	depth interval (cm)	Ca^{2+} (mg/l)	std	[DIC] (mmol/kg)	$\delta^{13}C_{DIC}$ (‰ VPDB)	[DIC] (mmol/kg)	$\delta^{13}C_{DIC}$ (‰ VPDB)	[DIC] (mmol/kg)	$\delta^{13}C_{DIC}$ (‰ VPDB)	[DIC] (mmol/kg)	$\delta^{13}C_{DIC}$ (‰ VPDB)	[DIC] (mmol/kg)	$\delta^{13}C_{DIC}$ (‰ VPDB)
13 m				June 2006		October 2006		December 2006		April 2006			
	B. W.	52.1	2.1	1.05	-7.0	1.15	-6.1	1.18	-7.2	1.36	-7.1		
	0 - 1	64.1	3.1	1.58	-11.5	1.31	-8.9	1.95	-10.2	1.82	-9.9		
	1 - 2	63.2	3.9	2.01	-12.6	1.57	-10.4	2.32	-12.6	2.18	-10.9		
	2 - 3	62.6	4.1	N.D.	N.D.	1.84	-9.8	2.74	-12.8	2.26	-11.4		
	3 - 4	62	4	N.D.	N.D.	1.76	-10.4	2.70	-12.9	2.96	-9.8		
	4 - 5	62.7	8	N.D.	N.D.	2.21	-9.5	2.53	-13.1	2.23	-10.3		
33 m				June 2006		July 2006		October 2006		February 2007		April 2007	
	B.W.	50.8	4.5	1.46	-7.8	1.23	-8.9	1.27	-7.9	1.37	-7.2	1.29	-7.0
	0 - 1	63.5	0.9	1.93	-10.5	1.63	-10.3	1.43	-9.8	1.94	-10.3	1.71	-9.6
	1 - 2	70.1	4.9	1.56	-12.2	2.35	-12.1	1.85	-11.9	2.31	-11.8	1.87	-9.8
	2 - 3	65.4	3.9	1.94	-12.0	1.80	-14.4	1.59	-13.2	2.47	-11.9	2.05	-10.5
	3 - 4	63.8	4	1.95	-12.7	1.85	-14.6	1.81	-12.7	2.44	-12.4	2.28	-11.0
	4 - 5	65.4	1.4	N.D.	N.D.	1.93	-14.7	2.03	-13.0	2.72	-13.4	2.52	-11.8
70 m				July 2006		December 2006		February 2007		April 2007			
	B.W.	46.2	1.2	1.48	-7.65	1.07	-8.09	1.44	-7.86	1.40	-7.46		
	0 - 1	57.7	3.8	1.74	-10.46	2.01	-9.12	2.39	-11.53	2.20	-11.29		
	1 - 2	57.1	2.3	N.D.	N.D.	2.19	-11.99	2.61	-12.07	2.93	-13.48		
	2 - 3	59.9	2.6	N.D.	N.D.	2.34	-13.71	3.14	-12.03	3.38	-13.40		
	3 - 4	60.7	3	1.92	-11.20	2.19	-11.38	3.12	-10.52	3.61	-12.15		
	4 - 5	61.2	3.4	2.05	-11.12	2.24	-10.69	3.24	-9.81	4.05	-9.82		

The coupling of aerobic respiration and carbonate dissolution implies that both processes can contribute to pore water DIC. Reaction (4.1) leads to a decrease of the pH, whereas, by removing the CO_2 molecules, reaction (4.2) buffers the solution. Since reaction (4.1) is assumed to be none reversal and because all CO_2 produced is consumed in equation (2), $\delta^{13}C$ value of the carbon added to pore water DIC by aerobic respiration equals the value of sedimentary organic matter (i.e., –26.7 to –27.9 ‰ VPDB, Table 4.2). Reaction (4.2) is also assumed to be irreversible. It is, therefore, assumed that no fractionation of carbon isotopes occurs during calcite dissolution. The $\delta^{13}C$ value of the carbon added to pore water DIC by calcite dissolution is, consequently, equal to the value of sedimentary carbonates (i.e., –1.23 to –2.64, Table 4.2).

Using $\delta^{13}C_{OM}$, $\delta^{13}C_{CaCO3}$, and $\delta^{13}C_{add}$ values, a simple mass balance allows us to evaluate the relative importance of organic matter remineralisation and calcite dissolution as source of DIC. For sediment without methanogenesis, approximately 45 % of DIC originates from calcite dissolution, whereas 55 % originates from remineralisation of sedimentary organic matter. This implies that the proportion of carbon added to the DIC issued from remineralisation of organic matter is higher than from calcite dissolution. This could simply be explained by the fact that reaction (4.1) is more important than reaction (4.2). This would effectively lead to an excess of ^{12}C in the DIC pool. In this case, pH decreases due to the enrichment of CO_2 in pore water. Still, the opposite is observed. A remineralisation of organic matter in sub- to anoxic conditions with reduction of nitrates and/or sulphates is more adapted to explain higher proportion of DIC originated from organic matter. Such reactions may also explain the increase in pH observed along sediment depth. Presence of nitrate and sulphate reduction in the studied sediment cannot be testified as sulphate, phosphate, ammoniac and hydrogen sulphide concentrations were not measured. However, both reactions are well known in soil, marine sediment, and lacustrine environments. Moreover, NO_3^-, NO_2^-, NH_4^+, SO_4^{2-} concentrations were measured in the sediment pore water of a 35 cm long core taken in Lake Geneva in front of Lausanne-Ouchy at 250 m water deep by Bolliger and co-authors (1992). Their results show that nitrates and sulphates disappear from pore water in the first centimetres of sediments whereas NH_4^+ concentration increases sharply, suggesting that all nitrates and sulphates are reduced in the first centimetres of sediment by microbial respiration during organic matter consumption. Based on the assumption that DIC added to the DIC pool in pore water originates from coupled aerobic respiration and carbonate dissolution (ratio reactions (4.1)/(4.2) = 1/1) and from respiration associated with reduction of nitrates and sulphates, it is possible to estimate the fraction of DIC added to the pore water issued from calcite dissolution, aerobic respiration and anaerobic respiration with reduction of sulphates and nitrates using a simple mass balance.

Results show that the proportions of the different carbon sources are very similar at the three depths with values ranging from 44.5 to 47.5 % of carbon issued from calcite dissolution (f_{CaCO3}), 44.5 to 47.5 % from aerobic respiration (f_{AOM}) and 8.6 to 11.2 % from anaerobic respiration with reduction of sulphates and

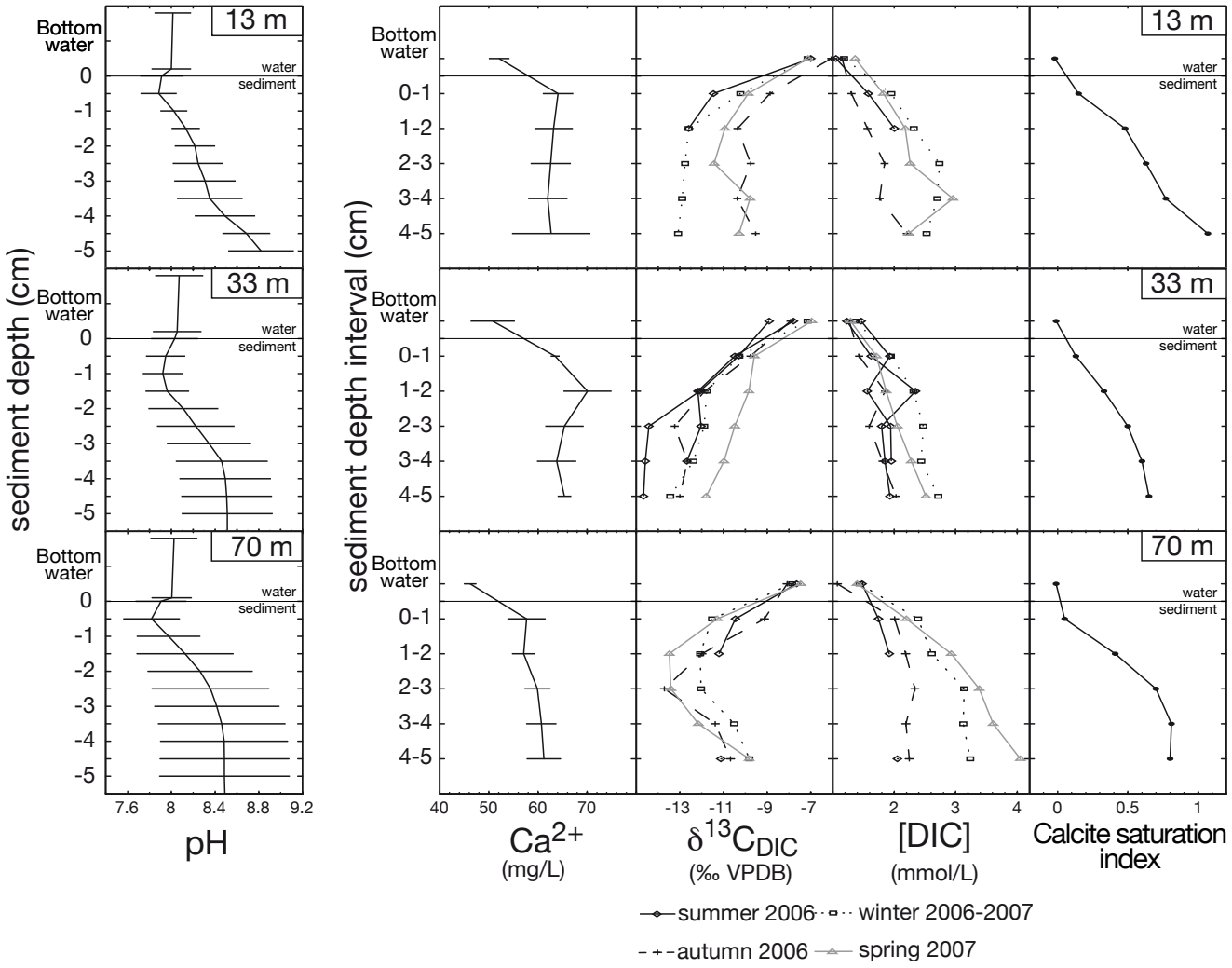


FIGURE 4.4
Geochemistry of interstitial water at site of 13, 33, and 70 m water depths: pH along sediment depth profiles, calcium concentration (Ca^{2+}), carbon isotope composition of dissolved inorganic carbon ($\delta^{13}C_{DIC}$), dissolved inorganic carbon concentration ([DIC]), and calculated calcite saturation index determined at the different sediment depth intervals. Horizontal lines for pH and Ca^{2+} plots represent standard deviations (1-sigma)

nitrates (f_{ROM}) (Table 4.5). This simple mass balance is able to explain the different trends observed in Figure 4.4 and gives realistic values.

For sediment with methanogenesis (from 3 to 5 cm sediment depth at 70 m), the value of the added DIC ($\delta^{13}C_{add}$) is higher because of the addition of CO_2 highly enriched in ^{13}C. This enrichment in ^{13}C reflects the strong isotopic fractionation between CH_4 and CO_2 during methanogenesis. There are two main methane formation pathways: acetate fermentation and CO_2 reduction, the former being generally the major pathway in freshwater sediment (Whiticar et al., 1986). The present database does not permit to distinguish both pathways, and methanogenesis was evaluated in the whole. Since there is no data on the carbon isotopic composition of CO_2 produced during methanogenesis in Lake Geneva, we estimated the probable range of isotopic composition of carbon issued from methanogenesis ($\delta^{13}C_{meth}$) using a $\delta^{13}C_{OM}$ equal to –28 ‰ VPDB (Table 4.2), a difference between $\delta^{13}C_{CO2}$ and $\delta^{13}C_{CH4}$ values ranging from 50 to 80 ‰ VPDB (Clark and Fritz, 1997), an isotopic enrichment factor between CO_2 and HCO_3^- of 10 ‰ (Szaran, 1997) and a ratio of 1 mole of HCO_3^- produced for 1 mole of CH_4 produced. This generates a probable $\delta^{13}C_{meth}$ value ranging between +7 to +34 ‰ VPDB. The proportion of the different sources of carbon added to DIC was estimated using a simple mass balance with the vales of $\delta^{13}C_{meth}$, $\delta^{13}C_{OM}$, $\delta^{13}C_{CaCO3}$, and $\delta^{13}C_{add}$, and the relations $f_{AOM} = f_{CaCO3}$ and $(f_{AOM} + f_{ROM}) / f_{CaCO3} = 1.249$ (relation get from results of sediment without methanogenesis at 70 m, Table 4.5). Results, shown in the last line of Table 4.5, indicate that an addition of approximately 1/7 to 1/3 of carbon produced by methanogenesis to pore water DIC permits us to explain the increase of $\delta^{13}C_{DIC}$ in the deepest sediments investigated at 70 m water

depth (Fig. 4.4) and higher values for $\delta^{13}C_{add}$ values in methanogenic sediments (Fig. 4.5). Comparison with other studies show that these results are typical for methanogenesis as source of carbon in sediment interstitial water DIC (Ogrinc et al., 2002, 2003).

In 2007, Walter and co-authors proposed that enrichment in ^{13}C of pore water could ensue from isotopic equilibration between CO_2 and carbonates via calcite dissolution-recrystallisation for grains having high specific surface area. For Lake Geneva, this phenomenon may be present but should not to be important for the DIC carbon isotope composition. Carbonates present in the sediment consist of detrital grains and of authigenic calcite. Both are presumed to have low specific surface area because grain sizes are relatively large and they have non-complex surfaces. Anyhow, methanogenesis is common in lacustrine sediments especially in deep sediment and is generally one of the major sources of DIC (LaZerte, 1987; Turner and Fritz, 1983; Whiticar et al., 1986; Hellings et al., 2000; Ogrinc et al., 2002). Methanogenesis is, therefore, a much simpler and convincing way to explain the variations observed in Lake Geneva sediment pore water.

To conclude, good oxygenation of deep water due to strong wind mixing and total winter overturn leads to elevated oxygen availability in surface layers of the sediments. Under these conditions, microbial aerobic respiration is favoured and the major sources of DIC originate from organic matter remineralisation and calcite dissolution. As oxygen gets depleted with depths in undisturbed sediment, sulphate and nitrate reducing bacteria take the lead and anaerobic remineralisation eventually contributes to carbon contribution to DIC, leading in the same time to an increase of the pH. The increase of f_{ROM} with water depth in Table 4.5 as well as the smaller slope in Figure 4.5 reflects that anaerobic respiration with reduction of sulphate and nitrate is favoured when oxygen supply decreases because of lower oxygen content in deep water and faster consumption of oxygen due to higher organic matter content in sediments with increasing water depths (Table 4.2). The generally higher availability of oxygen in the upper sediments prevents methanogenesis in the top part of the sediment at 13 and 33 m water depths. It does, however, occur in deeper part of the sediment investigated in the 70 m water depth site.

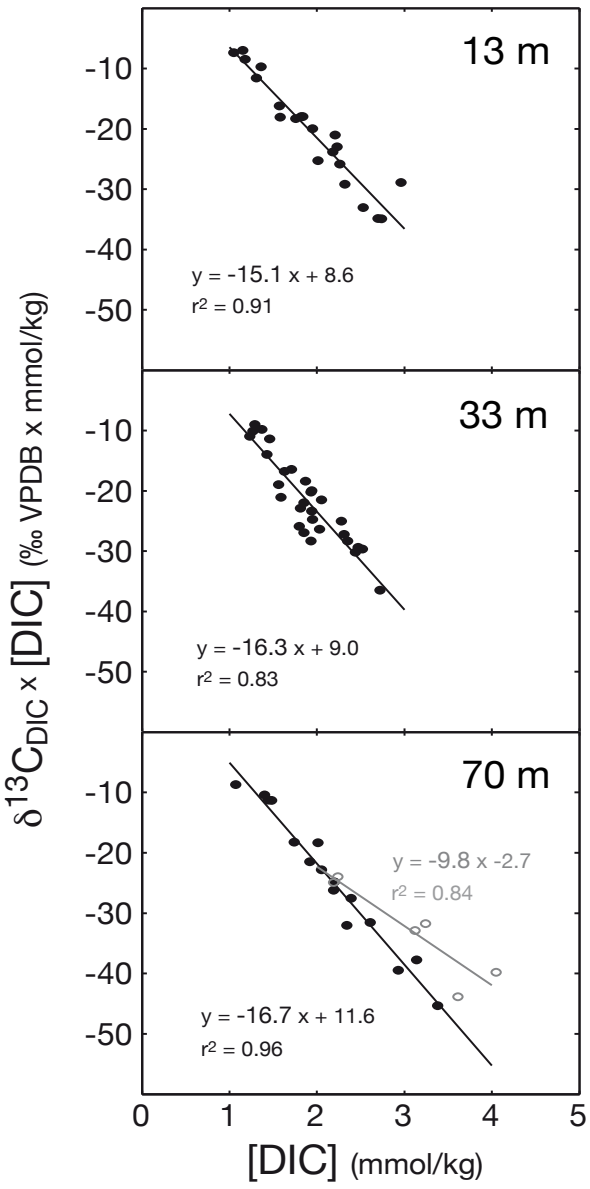


FIGURE 4.5
Plots of $\delta^{13}C_{DIC}$ • [DIC] versus [DIC] for the sediments without methanogenesis (in-filled black circles) and sediment with methanogenesis (unfilled gray circles) at 13, 33, and 70 m water depth. The slope of the linear regression line is the $\delta^{13}C$ value of the DIC added to the pore water ($\delta^{13}C_{add}$). See text for discussion.

TABLE 4.5
$\delta^{13}C_{add}$ values and importance of the different sources of DIC for pore water for non-methanogenic sediments (13 to 70 m) and methanogenic sediments (70 m meth.). f_{CaCO3} stands for DIC originated from dissolution of calcite, f_{AOM} for DIC originated from aerobic respiration, f_{ROM} for DIC originated from respiration with reduction of sulphates and nitrates, and f_{Meth} for DIC originated from methanogenesis.

site	$\delta^{13}C_{add}$ (‰ VPDB)	f_{CaCO3}	f_{AOM}	f_{ROM}	f_{METH}
13 m	-15.1	45.7%	45.7%	8.6%	-
33 m	-16.3	45.1%	45.1%	9.9%	-
70 m	-16.7	44.5%	44.5%	11.1%	-
70 m (meth.)	-9.8	30 to 38%	30 to 38%	8 to 10%	14 to 32%

2.2. Environmental Control on Ostracod Valve Geochemistry

Ostracod valve geochemistry is controlled by two types of parameters: 1) the factors that are controlled/influenced by the ostracod itself; and 2) the environmental factors that set the conditions in the macro- and microenvironments where ostracods calcify their valves.

Concerning the first point, biomineralisation is the main factor controlling ostracod valve geochemistry. The way ostracods calcify their valves controls the oxygen and carbon isotope fractionation as well as trace element partitioning during valve calcification. In brief, oxygen isotopic composition of ostracod calcite ($\delta^{18}O_{ostra}$) is not in equilibrium with that of water but presents a constant species-specific vital offset relative to the equilibrium value of calcite (von Grafenstein et al., 1999b; Keatings et al., 2002). Thus, apart from vital offsets, oxygen isotopic compositions of ostracod valves reflect the isotopic composition of water according to the temperature dependence of oxygen isotope fractionations of a calcite that crystallised under equilibrium (Kim and O'Neil, 1997). The carbon isotope composition of ostracods ($\delta^{13}C_{ostra}$) is believed to be in isotopic equilibrium with DIC (von Grafenstein et al., 1999, Keatings et al., 2002). Trace element partitioning in ostracod calcite has been studied for a long time and there are generally two interpretations: some authors argue that the partition coefficient between water and calcite can be used to describe trace element uptake during valve calcification with or without a relation to temperature, depending of the species and the type of environment (Chivas et al., 1986; Wansard et al, 1998; De Deckker et al, 1999; Wansard and Mezquita, 2001; Kondo, 2005). In contrast, other authors assert that trace element uptake is mainly controlled by the organism and follows the organisms metabolism, which is itself dependant on water temperature (Palacios-Fest & Dettman, 2001; Dettman et al, 2002). It is not the aim of this article to discuss these 'internal' processes and their importance on ostracod valve geochemistry. A more detailed study on isotopic fractionation and trace element uptake during ostracod valve calcification is presented in other manuscripts (*Chapter V-1* and *V-2*). Hence, the aim of this paper is to examine how the 'external' factors can influence ostracod valve geochemistry.

Figure 4.5 illustrates the different parameters that influence ostracod valve geochemistry and how they are interconnected. The 'biomineralisation' control on valve geochemistry is species dependant and is, at least for one site, independent of environmental conditions. The other factors, i.e. ostracod ecology and environmental conditions, are interconnected. Each species has a specific life-cycle and distinct (micro-)habitat preferences. The former determines the time of moulting of the valve whereas the latter controls the place where calcification occurs. Both 'fix' the environmental conditions, i.e., all the 'external' parameters such as water temperature, water geochemistry, pH, etc, prevailing during valve calcification. Another way to express this is to say that the ostracod valve geochemistry is influenced by the environmental condition through the ecology of the species, mainly its life cycle and habitat preferences (as well as diet).

In a general manner, there are two main configurations that control the interactions between ostracod autoecology and environmental conditions: 1) Epifaunal species in the littoral zones of the lakes; and 2) Infaunal species in profundal zones of the lake.

The littoral zone of the lake experiences large seasonal changes and ostracods encountered there are typically epifaunal and/or phytophylous (*Chapter III-2*). As

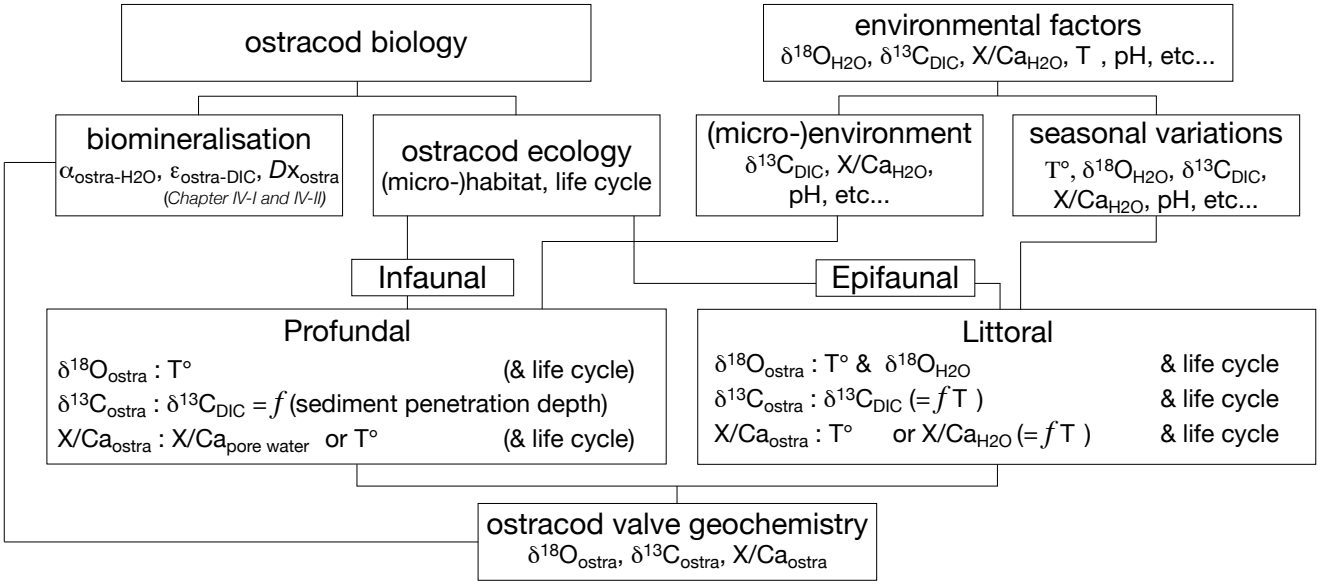


Figure 4.6
Summary of the different factors controlling ostracod valve geochemistry.

these types of ostracods live mainly on or above the surface of the sediment, the geochemistry of their valve will mainly be affected by seasonal variations of the environment and only in a minor way by (micro-) environmental conditions. Naturally, the effect of seasonal variations on the valve geochemistry will depend on the ostracod life cycle.

In contrast, seasonal variations are weak to insignificant in profundal zones and ostracods encountered there are mainly infaunal (*Chapter III-2*). As ostracods calcify their valves in sediments and seasonal variations are very weak, the conditions in the prevailing (micro-) environment controls their geochemistry.

The sublittoral zone is kind of intermediate to the above-mentioned zones. Both types of configurations described above are expected depending on taxon studied.

Keeping this model in mind as well as the observations mentioned in the preceding sections 2.1.2 and 2.1.3, the effect of the interconnection of the different factors on oxygen and carbon isotope compositions as well as the trace element contents of ostracod valves can be examined.

2.2.1. $\delta^{18}O_{ostra}$

For Lake Geneva, the oxygen isotopic composition of water ($\delta^{18}O_{H2O}$) is generally constant in space and time. The oxygen pool in interstitial water is much too large to be affected by the different reactions that take place in sediment interstices. In addition, enrichments in ^{18}O of littoral water by evaporation is restricted to the very surface layer and its effects are minimized by the mixing via the effects of wind. Therefore, oxygen isotope composition of ostracod valves ($\delta^{18}O_{ostra}$) is mainly controlled by water temperature during valve calcification according to specific life-history of the species.

2.2.2. $\delta^{13}C_{ostra}$

For infaunal species, especially in sublittoral to profundal zones, the carbon isotopic composition of the valves is mainly affected by the condition prevailing in the sediment interstices, i.e. the $\delta^{13}C_{DIC}$ values of interstitial water and its variability. The specific sediment penetration depth of the species also influences the final isotopic composition of the valves. In the studied sites, methanogenesis can not have an effect on ostracod valve geochemistry because: 1) living ostracods were generally not found in sediments affected by methanogenesis; and 2) $\delta^{13}C_{DIC}$ value of interstitial water in the zone where ostracods where mostly recovered (0 to 3 cm sediment depth, *Chapter III-2*) is mostly fixed by remineralisation of organic matter and carbonate dissolution.

For epifaunal species, especially in the littoral to sublittoral zones, the carbon isotope composition of the valve is mainly controlled by the seasonal variations according to the specific life-cycle of the

species and indirectly reflects the water temperature. A negative relationship between carbon and oxygen isotopic compositions of ostracod valves is, therefore, to be expected.

2.2.3. Trace element contents

Trace element contents of ostracod valves is affected in the same manner as their carbon isotopic composition, i.e., for infaunal species, especially in profundal and sublittoral zones, valves trace element content reflects mainly the Mg/Ca and Sr/Ca ratios of interstitial water and its variability, whereas valves of epifaunal species are influenced by seasonal variation of temperature and/or Mg/Ca and Sr/Ca ratios of bottom water, according to their specific life-cycle. Since Mg/Ca and Sr/Ca ratios of water and water temperature vary concomitantly in Lake Geneva, it may be difficult to determine which parameter between temperature and Mg/Ca and Sr/Ca ratios of water have the most important effect on valve trace element content.

Chapter V - 1 :

CONTROL ON OSTRACOD VALVE GEOCHEMISTRY: PART I. CARBON AND OXYGEN ISOTOPIC COMPOSITION

1. Introduction:

Ostracods are micro-crustaceans enclosed in a low-Mg calcite shell. Like other crustaceans, ostracods grow by successive moulting. Since calcite of the valve is surrounded by chitinous membranes, they fossilise easily and are well-preserved and numerous in the sedimentary archives (Oertli, 1975). Ostracod valves have, in addition, an advantage over bulk sediment for geochemical studies. By separating the ostracod valves from the sediment, only authigenic material can be analysed and any detrital influence avoided (Lister 1988). Furthermore, ostracods are benthic animals that can populate the deepest zones of lakes where water temperature is generally constant. In these conditions, variations of ostracod oxygen isotope compositions directly reflect changes of lake water isotope composition and thus climate (e.g. von Grafenstein, 2002).

Many palaeoenvironmental studies have used the stable isotope composition of ostracod fossils to reconstruct palaeoenvironmental conditions (von Grafenstein et al, 1999a; Ricketts et al., 2001; Schwalb, 2003; Belis and Ariztegui, 2004; Anadón et al., 2006; Tütken et al., 2006). The use of ostracod valves as geochemical archive is based on the assumption that the organism crystallised its carapace in equilibrium with water. In the case where a vital effect is present, it should be constant over a large range of environmental conditions. The presence of isotopic vital effects in ostracods was postulated in 1992 by von Grafenstein and co-authors. These authors suggested that it is phylogenetic. Growing ostracods in the laboratory, Xia and co-authors (1997) proved that ostracods do not crystallise at equilibrium but have $\delta^{18}O$ values higher than predicted for equilibrium growth. Studying living ostracods in German lakes, von Grafenstein and co-authors (1999b) were able to assess the vital effect of different species and stated that it was neither temperature nor water isotopic composition dependant. Later studies on living ostracods inhabiting an environment with constant geochemical and physical conditions confirmed these results (Keatings et al, 2002). The authors of the latter study suggested different mechanisms to be responsible for the non-equilibrium fractionation observed in ostracods in the light of previous results obtained from the inorganic calcium carbonate system (Kim et O'Neil, 1997; Zeebe, 1999). Although Keating and co-authors (2002) did not mention the point, vital offsets they obtained for oxygen is about 0.8‰ higher than the one determined by von Grafenstein and co-authors (1999b). This discrepancy corresponds to a non-negligible change in temperature of 3 °C and is beyond analytical uncertainties. First results on isotope composition of ostracod valves recovered from sediments of Lake Geneva showed the same discrepancy (Decrouy, 2004). Using vital offsets established by von Grafenstein and co-authors (1999b), the results obtained for oxygen isotope composition of adult *Candona neglecta* would imply that the valves had to crystallise at temperature lower than 4°C (even below 0°C for some samples), whereas temperature ranged between 4 to 6 °C during the calcification period (Decrouy, 2004). Hence, vital offsets in Lake Geneva is approximately 1‰ higher than predicted by von Grafenstein and co-authors (1999b). These preliminary results indicate the need to investigate in detail the stable isotope fractionation during ostracod valve calcification in Lake Geneva. This is also important if palaeoenvironmental reconstructions based on ostracod fossils are to be done. In addition, new knowledge on ostracod biomineralisation processes (Keyser and Walter, 2004) and on inorganic calcium carbonate systems (Kim et al., 2006, 2007) permits a re-evaluation of the different hypothesis proposed to explain isotopic non-equilibrium in ostracods, as well as to suggest several mechanisms that may be responsible for isotopic non-equilibrium calcite formation in ostracod.

In the present study, the stable isotope compositions of living ostracods belonging to 15 species collected at one-month intervals during a one-year cycle at five sites from 2 to 70 m water depths is examined. Detailed knowledge on ostracod autoecology (*Chapter III-1 and III-2*) and environmental parameters (*Chapter IV*) forms the basis to interpret

these results. The relation between ostracod oxygen isotope composition and oxygen isotope composition of water as well as water temperature was examined in detail for juveniles and adult males and females at different depths. Precise knowledge on the species-specific life-cycles permitted the evaluation of oxygen isotope fractionations. Carbon isotope composition of ostracod fossil valves is generally more difficult to interpret (e.g., Schwalb, 2003; Filippi et al., 1999) and often not discussed at all. The complex interaction between variations of dissolved inorganic carbon (DIC) isotope composition in microenvironments and the species microhabitat preferences may explain in part the apparent non-coherence observed in ostracod carbon isotope compositions (e.g., von Grafenstein et al., 1999b; *Chapter IV*). Here, special attention was paid to the relation between ostracod autoecology (life-cycle and microhabitat preferences) and carbon isotope composition. This approach allows the different biological and environmental controls on carbon isotopic composition of ostracods valves to be evaluated.

2. Determination of Oxygen Isotope Fractionation Factor and Calculations for the Isotopic Composition of an Equilibrium Calcite

Differences between the δ values of two chemical phases, X and Y, may be expressed using the isotopic fractionation factor ($\alpha_{X\text{-}Y}$) where

$$\alpha_{X\text{-}Y} = (1000 + \delta_X)/(1000 + \delta_Y) \qquad (5.1a)$$

or the isotope enrichment factor ($\varepsilon_{X\text{-}Y}$) where

$$\varepsilon_{X\text{-}Y} = (\alpha_{X\text{-}Y} - 1) \bullet 1000 \qquad (5.1b)$$

The isotope enrichment factor can be further approximated by

$$\varepsilon_{X\text{-}Y} \approx \Delta_{XY} = \delta_X - \delta_Y \qquad (5.1c)$$

2.1. Determination of Oxygen Isotope Fractionation Factor and Oxygen Isotope Composition of Calcite Grown Under Equilibrium

Knowing the oxygen isotope composition of water and calcite, the oxygen isotope fractionation factor ($\alpha_{calcite\text{-}water}$) can be calculated using equation (5.1a), rewritten for oxygen isotope compositions of water and calcite:

$$\alpha_{calcite\text{-}water} = (1000 + \delta^{18}O_{calcite})/(1000 + \delta^{18}O_{water}) \qquad (5.1d)$$

where $\delta^{18}O_{calcite}$ and $\delta^{18}O_{water}$ are the respective oxygen isotope composition of calcite and water expressed using delta notation relative to VSMOW. To convert $\delta^{18}O$ values given relative to VPDB to those relative to VSMOW, the expression suggested by Coplen and co authors (1983) was used:

$$\delta^{18}O_{VSMOW} = 1.03091 \bullet \delta^{18}O_{VPDB} + 30.91 \qquad (5.2)$$

$\alpha_{calcite\text{-}water}$ is temperature dependent. This dependency can be expressed using many different relations. Here, the expression suggested by Kim and O'Neil (1997) was used. Hence, the relation between $\alpha_{calcite\text{-}water}$ and temperature can be written as follow:

$$1000 \bullet \ln \alpha_{calcite\text{-}water} = a \bullet (1000/T) - b \qquad (5.3a)$$

where T is the water temperature in Kelvin and a and b are unknown coefficients that must be determined using experimental data. The study of Kim and O'Neil (1997) suggests the following expression:

$$1000 \bullet \ln \alpha_{calcite\text{-}water} = 18.03 \bullet (1000/T) - 32.42 \qquad (5.3b)$$

If oxygen isotope compositions of water and temperature are known, the expected $\delta^{18}O$ value of calcite grown under equilibrium can be assessed using expression (5.1d) and (5.3b).

2.2. Determination of Carbon Isotope Composition of Calcite Grown Under Equilibrium

The model proposed by Keatings et al. (2002) was used to calculate the expected carbon isotope composition of calcite grown in equilibrium with water.

The water's total dissolved inorganic carbon (DIC) may be regarded as a mixture of dissolved CO_2, HCO_3^-, and CO_3^-. For simplicity we will denote these three species as a, b, and c, and their $\delta^{13}C$ values as δ_a, δ_b, and δ_c, respectively.

If f is the concentration of a species as a fraction of the DIC, and noting that $f_a + f_b + f_c = 1$, then for isotope mass balance:

$$\delta_{DIC} = f_a \bullet \delta_a + f_c \bullet \delta_c + (1 - f_a - f_c) \bullet \delta_b \qquad (5.4a)$$

Using enrichment factors to express the $\delta^{13}C$ value of a carbon species in terms of its difference from that of HCO_3^-, and noting that the approximation $\varepsilon_{X\text{-}Y} \approx \delta_X - \delta_Y$ is accurate enough for the carbon isotope enrichment

factors used here, the following relationship can be derived:

$$\delta_{calcite} = \delta_{DIC} + \varepsilon_{calcite-b} - (f_a \bullet \varepsilon_{a-b} + f_c \bullet \varepsilon_{c-b}) \quad (5.4b)$$

This relationship will be used to calculate the expected equilibrium $\delta^{13}C$ values for calcite from measurements of the $\delta^{13}C$ value of the DIC, determination of carbon speciation (f) based on the water chemistry, and published determinations of the equilibrium enrichment factors (Romanek et al., 1992; Zhang et al., 1995)."

3. Data Processing and Results

Carbon and oxygen isotope compositions of ostracod valves ($\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$) were determined for 15 species belonging to family Candonidae (*Candona candida*, *Candona neglecta*, *Fabaeformiscandona caudata*, *Pseudocandona compressa*, and *Cypria ophtalmica*), family Cyprididae (*Prionocypris zenkeri*, *Herpetocypris reptans*, *Isocypris beauchampi*, *Cypridopsis vidua*, *Plesiocypridopsis newtoni*, *Potamocypris similis*, and *Potamocypris smaragdina*), and superfamily Cytheroidea (*Limnocythere inopinata*, *Limnocytherina sanctipatricii*, and *Cytherissa lacustris*). Given the space restrictions, only representative results are given in this chapter. Complete lists of raw results can be found in *Appendix II*. *Candona candida* was chosen here as representative (see Table 1 and Figures 5.1, 5.2, and 5.3).

3.1. Oxygen Isotope Results

To examine the relation between the oxygen isotope compositions of ostracods ($\delta^{18}O_{ostra}$) and water ($\delta^{18}O_{H2O}$), and water temperature, it is necessary to estimate the oxygen isotope composition of the water in which the ostracod moulted and the temperature at the time of valve calcification (T_c). $\delta^{18}O_{H2O}$ values measured throughout the year are very stable, ranging from approximately –12.3 to –12.5 ‰ VSMOW. Water temperature, in contrast, varies strongly, especially in the littoral zone where temperatures range from 2.1 to 28°C. Very precise data are available for water temperature as they were measured continuously. On the base of this dataset, average temperature preceding the sampling can be calculated for different periods of time (from one day to several months). Still, the exact time at which ostracods moulted (i.e., time of valve calcification) is unknown and has to be estimated. A first estimation can be done on the basis of the species autoecology. The life-cycles were studied for all species found in the "Petit-Lac" (see *Chapter III-1 and III-2*). The life-cycle of *C. candida* is illustrated in Figure 5.1 C and D. On the basis of these diagrams, it is possible to postulate the time during which moulting occurs. For example, moulting periods of the last juvenile stage A-1 to adult at 13 m water depths begins in November. As no specimen of the last juvenile stage A-1 were found after December, all adults found after January must have reached maturity between November and January and survived until being sampled. Detailed knowledge of species life-cycles thus permits to restrict the period of moulting. It is, therefore, possible to constrain more precisely water temperature during valve calcification.

In parallel, water temperature during valve calcification can be estimated using a 'best fit' correlation method. While the exact time during which the valve was calcified is unknown, it is safe to assume that the ostracods moulted at a precise time during a certain period of time preceding the sampling. This is correct only because living ostracods were analysed. Moreover, for a high number of specimens analysed or relatively constant temperatures, mean temperature preceding sampling must reflect the temperature prevailing during valve calcification. Thus, average temperature can be used to approximate the real calcification temperature. Mean temperatures were calculated on the basis of increasing time preceding sampling, with the value for 1 day corresponding to mean water temperature over the 24 hours preceding sampling, the value for 1 week corresponding to mean water temperature over the 7 days preceding sampling, and so on. Average temperatures were calculated for 1, 2, 3, 4, 5, and 6 days – 1, 2, and 3 weeks – 1, 2, 3, 4, 5, and 6 months. The lapse of time used for the calculation (for example 3 weeks) is referred as 'calcification time'.

For carbonates crystallised under equilibrium, oxygen isotope fractionation ($\alpha_{calcite-water}$) is inversely proportional to temperature. At low temperature, $10^3 \ln\alpha_{calcite-water}$ is proportional to $10^3/T$ (Kim and O'Neil, 1997). Hence, if ostracod calcite grows in equilibrium with a constant 'vital offset' as suggested by several authors (von Grafenstein et al., 1999b; Keatings et al., 2002), then, $10^3 \ln\alpha_{calcite-water}$ must plot linearly against $10^3/T$. Under this assumption, the higher the correlation coefficient (r^2) between $10^3 \ln\alpha_{calcite-water}$ and $10^3/T$ values is, the better the estimation of T_c is.

TABLE 5.1
Geochemical data of adult and juvenile *Candona candida* (see text for explanation).

depth	age	sampling		analyses identifier	valve labels	area 44/45 /46	$\delta^{13}C$-ostracod	int. std.	ext. std.	$\delta^{18}O$-ostracod	int. std.	ext. std.	mean period for Tc	T_c	Date $\delta^{18}O$-water	$\delta^{18}O$-water	$\alpha_{calcite-water}$	vital offset	$\delta^{18}O$ calc. T_c	date X/Ca-water	Mg/Ca-water	accepted Mg/Ca-ostracod	D_{Mg}	Sr/Ca-water	accepted Sr/Ca - ostracod	D_{Sr}
(m)						(mV)	(‰ VPDB)			(‰ VPDB)				°C		(‰ VSMOW)		(‰)	(°C)		molar ratio	molar ratio		molar ratio	molar ratio	
33	Ad	O	10.25.06	o331	1 to 4	1.4	-3.25	0.32	0.18	-7.33	0.29	0.15	2 w.	7.3	1 m.	-12.31	1.0361	3.75	5.5	1 m.	-	-	-	0.00478	0.00187	0.392
		Q	11.28.06	o274	5 to 10	6.0	-6.64	0.10	0.06	-8.18	0.14	0.08	1 m.	8.4	1 m.	-12.38	1.0353	3.12	8.9	1 m.	0.216	0.00396	0.0183	0.00486	0.00144	0.295
		S	01.09.07	o275	11 to 18	9.0	-6.54	0.06	0.06	-8.37	0.08	0.08	O.T.	-	nov 07	-12.38	1.0351	-	9.7	-	-	-	-	-	-	-
		U	02.15.07	o276	19 to 24	6.5	-6.56	0.10	0.06	-8.15	0.07	0.08	O.T.	-	nov 07	-12.38	1.0353	-	8.7	-	-	-	-	-	-	-	-
		W	03.12.07	o332	25/26	2.1	-6.35	0.17	0.18	-8.06	0.21	0.15	O.T.	-	nov 07	-12.38	1.0354	-	8.3	-	-	-	-	-	-	-	-
		Y	04.10.07	o333	27/28	1.9	-6.47	0.14	0.18	-8.18	0.33	0.15	O.T.	-	nov 07	-12.38	1.0353	-	8.9	-	-	-	-	-	-	-	-
		aa	05.01.07	o334	29/30	1.9	-7.08	0.26	0.18	-7.96	0.17	0.15	O.T.	-	nov 07	-12.38	1.0355	-	7.9	-	-	-	-	-	-	-	-
	A-1	M	10.04.06	o343	1 to 4	1.5	-5.89	0.20	0.21	-7.91	0.49	0.14	2 m.	7.2	1 m.	-12.49	1.0357	3.24	7.2	1 m.	-	-	-	0.00486	0.00143	0.294
		O	10.25.06	o344	5 to 10	2.2	-6.00	0.18	0.21	-7.99	0.27	0.14	2 m.	7.4	1 m.	-12.31	1.0354	3.03	8.4	1 m.	-	-	-	0.00478	0.00144	0.301
	A-2	I	07.24.06	o406		1.1	-7.18	0.25	0.16	-7.69	0.45	0.14	3 w.	7.1	1 m.	-12.43	1.0359	3.28	6.5	sampl.	-	-	-	0.00482	0.00088	0.182
		K	08.31.06	o407		1.4	-6.33	0.27	0.16	-7.78	0.31	0.14	3 w.	7.0	1 m.	-12.33	1.0357	3.33	7.3	sampl.	-	-	-	0.00486	0.00090	0.185
		M	10.04.06	o408		1.9	-6.99	0.37	0.16	-7.77	0.30	0.14	3 w.	7.3	1 m.	-12.49	1.0358	3.21	6.6	sampl.	-	-	-	0.00478	0.00149	0.311
13	Ad	F	06.12.06	o335	1/2	2.3	-6.31	0.16	0.18	-8.25	0.20	0.15	O.T.	-	1 m.	-12.45	1.0353	-	8.9	1 m.	-	-	-	0.00398	0.00148	0.372
		P	11.15.06	o336	3 to 6	3.2	-3.76	0.12	0.18	-9.18	0.17	0.15	1 m.	14.0	1 m.	-12.38	1.0343	3.38	13.4	1 m.	-	-	-	0.00425	0.00192	0.453
		R	12.12.06	o337	7/8	1.8	-4.33	0.24	0.18	-8.20	0.28	0.15	1 m.	10.3	1 m.	-12.26	1.0351	3.41	9.5	1 m.	-	-	-	0.00495	0.00175	0.353
		T	01.16.07	o338	9/10	2.0	-6.09	0.22	0.18	-8.11	0.23	0.15	3 m.	7.8	1 m.	-12.21	1.0352	2.89	9.4	1 m.	-	-	-	0.00496	0.00156	0.314
		X	03.27.07	o339	11/12	2.1	-6.85	0.15	0.18	-8.43	0.17	0.15	O.T.	-	jan 07	-12.21	1.0349	-	10.8	-	-	-	-	-	-	-	-
	A-1	P	11.15.06	o345	3 to 12	4.1	-5.39	0.16	0.10	-9.76	0.13	0.06	2 m.	14.4	1 m.	-12.38	1.0337	2.87	16.1	1 m.	0.227	0.00280	0.0123	0.00425	0.00161	0.379
		R	12.12.06	o346	13 to 16	1.8	-5.40	0.44	0.21	-9.17	0.34	0.14	2 m.	12.4	1 m.	-12.26	1.0341	2.90	14.0	1 m.	-	-	-	0.00495	0.00149	0.302
	A-2	F	06.12.06	o401		2.0	-5.39	0.28	0.05	-8.59	0.19	0.03	3 w.	10.3	1 m.	-12.45	1.0349	3.17	10.4	sampl.	-	-	-	0.00430	0.00163	0.380
		H	07.11.06	o402		3.8	-5.75	0.13	0.08	-9.01	0.19	0.06	3 w.	13.1	1 m.	-12.40	1.0344	3.36	12.6	sampl.	-	-	-	-	-	-
		J	08.10.06	p403		3.7	-5.17	0.15	0.08	-9.30	0.10	0.06	3 w.	14.4	1 m.	-12.39	1.0341	3.25	13.9	sampl.	-	-	-	0.00486	0.00152	0.313
		L	09.12.06	o404		3.0	-6.17	0.14	0.05	-9.22	0.25	0.03	3 w.	14.9	1 m.	-12.30	1.0341	3.43	14.0	sampl.	-	-	-	0.00392	0.00135	0.345
		N	10.10.06	o405		4.8	-5.68	0.08	0.08	-9.28	0.12	0.06	3 w.	14.6	1 m.	-12.28	1.0340	3.40	14.3	sampl.	-	-	-	0.00425	0.00146	0.344

Inspection of all values often reveals that some points fall systematically off a linear distribution of the values. It is considered that these outliers do not reflect the conditions prevailing before sampling. This is the case for the valves collected at the end of March at 13 m (sampling X), which have a $10^3 ln\alpha_{calcite\text{-}water}$ value reflecting a high water temperature. These valves were sampled after a period of low water temperature (small black square on Figure 5.1 B with 1000/T = 3.573 and $1000 ln\alpha_{(calcite\text{-}water)} = 34.6$). It is obvious on the basis of the species life-cycle that this sample contains valves that must have calcified between November and January while the temperature was higher. This sample is, therefore, discarded and labelled as Out of Time (O.T.) in the database (see Table 5.1). Once all O.T. samples discarded, the correlation coefficient between $10^3 ln\alpha_{calcite\text{-}water}$ and $10^3/T$ is generally already satisfactory. For *Candona candida*, for example, coefficient factor r^2 is 0.75 with the O.T. values, but get to 0.90 when these are discarded.

Estimates of calcification temperature can be further refined with a slightly different 'calcification time' based on the species life-cycle. For species that develop continuously (permanent forms) or species that have a development spread over a long period, there is no reason to apply these exceptions. But, certain species have very clear-cut development. For these species, the dataset must be closely inspected to detect discrepancies between life-cycle and estimated 'calcification time'.

Non-coherence between these two parameters can arise because of several causes. For certain species, specific environmental conditions, mainly water temperature, have to be fulfilled before the animal can moult in adult stage. Once the limiting requirements are fulfilled, development resumes and adults appear 'instantaneously'. The 'calcification time' is generally on the order of one to several months. However, for the first adults to appear (or any new specimens of another development stage) the 'calcification time' can not be greater than 1 month and the 'calcification time' must be significantly shorter. For these types of samples, different 'calcification times' are determined on the basis of the species life-cycle. Sample O at 33 m (see Figure 5.1 D and Table 5.1) examples for such a case. Another exemple is the last occurrence of specimens of a certain development stage. Adults sampled at 13 m during session T must have crystallised from November to January (Fig 5.1 C). For this sample, 'calcification time' must be longer than thus for the other adults. Hence, a 'calcification time' of three months was chosen for this sample on the basis of the species life-cycle (Table 5.1).

It is thought that these adjustments permit more precise estimates of the 'calcification temperature' because they are supported by life–cycle information and not simply arbitrarily set. If such an adjustments are not supported by the life-cycle, the data points are retained as is and included in the dataset used for the regression.

A last optimisation can be done by adopting slightly different 'calcification times', without changing the 'calcification times' for the two cases mentioned above. Different values for the isotopic composition of water, i.e. using the value measured at the time of sampling or values of previous sampling sessions, naturally in accord with estimated 'calcification time' can be used. These last modifications change the coefficients for the best-fit regression line only slightly. For *Candona candida*, for example, the coefficients are a = 18.23 and b = –30.07 and $r^2 = 0.90$ when the $\delta^{18}O_{H2O}$ values used to calculate the fractionation factors correspond to the sampling date. When the $\delta^{18}O_{H2O}$ values used to calculate the fractionation factors correspond to the value of the prior month, the coefficient are a = 18.01 and b = –29.15 and $r^2 = 0.92$. Thus, using different $\delta^{18}O_{H2O}$ values lead to a change of a 1 to 3 % of the regression coefficients for this species.

All these manipulations were at first effectuated independently for each site and for each development stage. If the obtained regression lines for the different sites and the different development stages and/or gender were similar, values were treated together and a unique regression line was calculated for the species. For all species, no differences were detected between the different sites. Fractionation factors are equivalent for females and males as well as for the different development stages, except in the case of *Herpetocypris reptans*. The homogeneity of the fractionation factors obtained for the different sites and the different development stages can be assessed on Figure 5.1. These results are in agreement with a previous study that observed no significant differences between the different instars (von Grafenstein et al., 1999b). A unique expression for oxygen isotope fractionation is therefore determined for each species using equation (5.3a). The reason why oxygen fractionation is different among juveniles and adults of *Herpetocypris reptans* is yet unclear, but may be linked to the large size of this species compared with other common freshwater species.

Using equations (5.1d) and (5.3a), measured $\delta^{18}O_{H2O}$ values, and measured $\delta^{18}O_{ostra}$ values, it is possible to recalculate water temperature during valve calcification for each sample ('$\delta^{18}O$ calc. T_c' in Table 5.1). Results for *C. candida* are compared to water

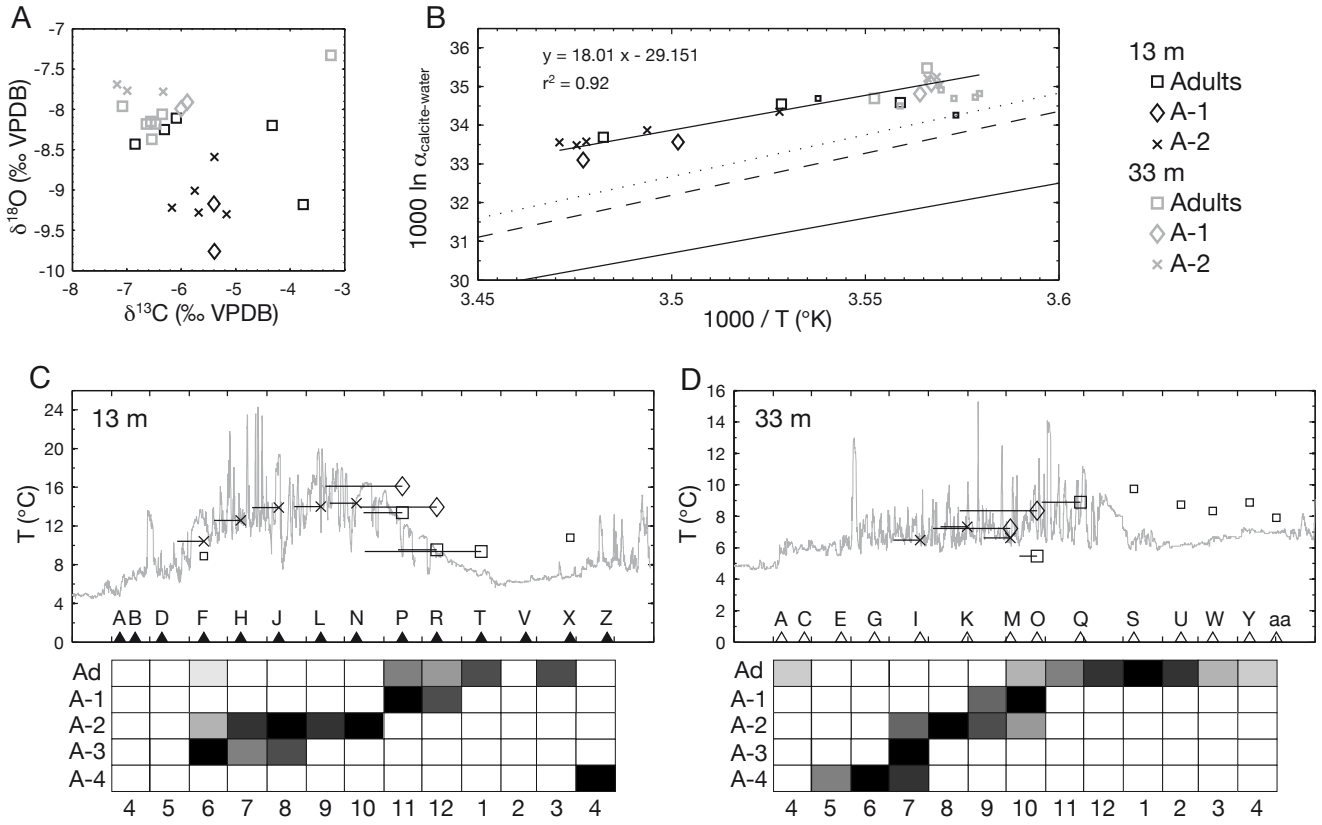


FIGURE 5.1
Oxygen isotope composition of adult and juvenile valves of *Candona candida*: (A) Oxygen versus carbon isotopic compositions; (B) Oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus 'estimated' valve crystallization temperatures; (C) water temperature at 13 m water depth and '$\delta^{18}O$ recalculated' crystallization temperatures with subjacent illustration of the ostracod life cycle; (D) same as (C) but for 33 m water depth. Smaller markers stand for samples not considered for linear regression calculations (see text for explanations).

temperature on Figure 5.1 C and D. The horizontal bars in the graphs represent 'calcification time'. This kind of representation, together with the subjacent life-cycles, permits the pertinence of determined 'calcification time' to be tested. Note that same graph can be construct using only the raw data, $\delta^{18}O_{ostra}$ being placed on a second inverse Y-axis and adjusted to the water temperature record. For both Y-axis scales, the relation 1 ‰ ≈ 0.25 °C has to be used. Naturally, this is possible because $\delta^{18}O_{H2O}$ values vary only insignificantly in comparison with water temperature.

A final point to made for Figure 5.1 B is that the solid, dashed, and dotted lines crossing obliquely the plot represent the isotopic fractionation factor of inorganic calcite crystallised in solution of 5, 15 and 25 mM of calcium, respectively (Kim and O'Neil, 1997). These authors consider, for several reasons, that calcite grown in the most dilute solution, i.e. 5 mM of Ca^{2+}, crystallised in equilibrium with water. Hence, the bold line is interpreted to represent the equilibrium for the water-calcite system. The two dashed lines were, in contrast, interpreted as non-equilibrium fractionation by the authors. The three lines obtained for the different concentrations are shown in all $10^3 ln\alpha_{calcite\text{-}water}$ versus $10^3/T$ graphs for comparison with the oxygen isotope fractionation among different ostracod species and between ostracods and synthetic calcite.

To conclude, information given in Figure 5.1 permits the oxygen isotope data to be evaluated and summarised. An identical figure is given for each species. All figures can be consulted in *Appendix I* of the present thesis.

3.2. Carbon Isotope Results

During preliminary examinations, the $\delta^{13}C$ values of the ostracods were compared with monthly $\delta^{13}C_{DIC}$ values. Yet, no significant correlations were found between $\delta^{13}C_{ostra}$ and $\delta^{13}C_{DIC}$ values corresponding to the sampling date or preceding dates. This does not necessarily mean that ostracod valve $\delta^{13}C$ values

are not in equilibrium with $\delta^{13}C$ values of the DIC. But it can be explained in at least two ways: (1) the $\delta^{13}C_{DIC}$ values measured once every month only do not reflect the precise $\delta^{13}C_{DIC}$ value prevailing during valve calcification or (2) the $\delta^{13}C_{DIC}$ values measured in the water overlying the sediment is not equal to the $\delta^{13}C_{DIC}$ value in the micro-environment where calcification occurred. These two possibilities will be further discussed as follows:

(1) Validity of the first hypothesis is supported by environmental conditions. A significant correlation was found between monthly $\delta^{13}C_{DIC}$ values measured at 2, 5, and 13 m water depths and the water temperature at time of sampling (r^2=0.79, n=12 for 2 m; r^2=0.37, n=12 for 5 m; r^2=0.81, n=12 for 13 m;). The correlation is absent when monthly $\delta^{13}C_{DIC}$ values are compared with mean temperature calculated for 1 or more days preceding sampling. This suggests that $\delta^{13}C_{DIC}$ values reflect the condition at the very precise moment of sampling and not the mean conditions prevailing during the preceding periods. This also implies that the values may vary passably from one day to the next (for a detailed discussion, see *Chapter IV*). As samples for $\delta^{13}C$ measurements contain one to tens of valves, the $\delta^{13}C_{ostra}$ value reflects the condition prevailing during a precise day in the case where 1 ostracod is analysed to the mean conditions existing during the moulting period in the case where many valves are analysed and where valves were formed on different days of moulting. In both cases, monthly $\delta^{13}C_{DIC}$ values can not be used to estimate the $^{13}C_{DIC}$ values prevailing during valve calcification. However, positive correlations between $\delta^{13}C_{ostra}$ values and 'calcification temperature' are obtained for certain species (*Appendix I*). As $\delta^{13}C_{DIC}$ and water temperature are positively correlated (*Chapter III*), this observation supports the hypothesis that $\delta^{13}C_{ostra}$ values reflect $\delta^{13}C_{DIC}$ values during valve calcification. Actually, $\delta^{13}C_{DIC}$ values during valve calcification might be more accurately estimated by water temperature than by monthly $\delta^{13}C_{DIC}$ values.

Consequently, $\delta^{13}C_{ostra}$ values were not examined as a function of their sampling dates in order to assess the carbon isotope fractionation but examined as annual means. Box plots (minimal value, 1st quartile, median (bold line), average (fine line), 3rd quartile, and maximal value) were used in Figure 5.3 to represent the carbon isotope composition of females, males, adults, and A-1 and A-2 juvenile stages of Candonidae, Cyprididae, and Cytheroidea.

(2) Concerning the second point, it is evident that $\delta^{13}C_{ostra}$ values should be compared to $\delta^{13}C_{DIC}$ values of the ambient water within which the ostracod calcified its carapace. Hence, assessing the spatial variability of $\delta^{13}C_{DIC}$ values is crucial for this point. Sampled water consists of water lying few centimetres above the sediment-water interface ('bottom water'). Thus, the monthly $\delta^{13}C_{DIC}$ values reflect conditions of 'open water', which, because of the action of waves and bottom currents, are likely to be quite homogenous. Ostracods are benthic animals and we can assume that location where calcification occurs is fixed by the species-specific micro-habitat preferences. $^{13}C_{DIC}$ values in these micro-environments can be quiet different compared to those in 'open water'. For example, phytophilous species live generally on algae. Due to the photosynthetic activity of the latter, the DIC surrounding the ostracod in this microenvironment can be depleted in ^{12}C and presents, therefore, higher $\delta^{13}C_{DIC}$ values than 'open water'. In contrast, infaunal species live burrowed within the sediment, where water DIC can be strongly affected by release of CO_2 enriched in ^{12}C due to remineralisation of organic matter. Epifaunal habitat (i.e. living on the surface of the sediment) presents the same problems because DIC at the sediment-water interface can be strongly affected by diffusion from underlying sediment. Nevertheless, it is possible to get an idea on the mean $\delta^{13}C_{DIC}$ values of interstitial water at the three deepest sites (13, 33, and 70 m). A detailed discussion on sediment interstitial pore water geochemistry can be found in *Chapter III* of the present thesis.

To examine whether ostracod valves crystallised in equilibrium with DIC or not, the $\delta^{13}C_{ostra}$ values are compared to the $\delta^{13}C$ values of a calcite ($\delta^{13}C_{CaCO3}$) that precipitates in equilibrium with DIC according to equation (5.4b) in Figure 5.3. $\delta^{13}C_{CaCO3}$ values were calculated for all monthly water samples and for interstitial water samples using the measured $\delta^{13}C_{DIC}$ values, pH, and temperature. To represent the seasonal variation, monthly $\delta^{13}C_{DIC}$ values are given as circles where the diameters are proportional to the water temperature during sampling.

4. Discussion

4.1. Biomineralisation in Ostracods: State of the Art

Biomineralisation in ostracods has not been as intensely studied, as is the case for other organisms such as foraminifera, corals, or microbial mats (e.g., Dove et al., 2003). However, several studies revealed

essential points on ostracod biomineralisation (e.g., Turpen and Angel, 1971; Keyser and Walter, 2004). In order to discuss the different mechanisms that may account for isotopic fractionation during valve calcification, it is necessary to briefly describe what is known about ostracod valve structure and biomineralisation processes.

The carapace of ostracods consists of two dorsally articulated valves, which in most groups, including all freshwater species, are mineralised with low magnesium calcite (Kesling, 1951; Sohn, 1958). Like other crustaceans, ostracods develop by successive moulting (ecdysis). Only the last stage (the adult) is fully formed and sexually mature, but all development stages possess a more or less calcified cuticle. At each moult, the cuticle and the carapace is shed and discarded. A new carapace is calcified in a period of a few hours (Turpen and Angel, 1971) to a few days (Roca and Wansard, 1997). Turpen and Angel (1971) showed that, in *Herpetocypris*, the calcium in the valve is derived from the ambient water and neither recycled during moulting nor stored in the animal prior to moulting. Fassbinder (1912) was able to culture fully calcified *Cypridopsis vidua* in calcium free water, suggesting that metabolic sources of calcium and metabolic fluids might also play a role in the formation of valve calcite. The calcified shell consists of small crystallites embedded in a chitinous and protein matrix (Bate and East, 1972, 1975; Langer, 1973; Rosenfeld, 1979; Keyser, 1982). Depending on the systematic relationship, the microstructure of the adult carapace is expressed in a variety of forms. The shell can be completely built of calcite crystals as in Cytheroidea, or composed of parallel chitinous lamellae together with a layer of crystallites as in Cypridoidea (Keyser and Walter, 2004). On the basis of SEM pictures and XRF-analyses effectuated on animals selected at different times during the moulting process, the latter authors proposed a general succession of processes to achieve valve calcification: "Prior to moulting, the ostracods begin producing shells by storing a huge amount of calcium phosphate granules together with chitin precursors in the outer epidermal cells. These granules release their contents into the extra-cellular space directly outside the epidermal cells. This material is transformed into small platelets, each about the size of one granule. The platelets are no longer made of calcium phosphate but of calcium carbonate. These platelets disintegrate into small granular structures, which appear to be amorphous calcite. This granular substance then forms the crystals, which, in connection with chitin and proteins, build the shell of the ostracods. This final step is not achieved in some species, for instance in the genus *Cypria*, and the shell consist mainly of amorphous material. However, shells of adult specimens of other genera have totally crystallised and no amorphous materiel is left. In the larval stages, on the other hand, crystallisation is not complete and the animals have weaker shells" (Keyser and Walter, 2004).

Besides biomineralisation processes, some morphological and geochemical particularities are of interest in the present discussion. Growth rate and calcification are both influenced by water temperature. In general, development is faster at high temperature, i.e. the time between successive moults is shorter and life span is shorter (Geiger, 1990a). Ostracods bred in the laboratory at relatively low temperatures with respect to the species autoecology, have low survival rates associated with slow development and weak calcification (Xia et al, 1997; Mezquita et al., 1999a). Calcification processes were also much slower in these conditions and may account for the latter observations (Roca and Wansard, 1997). On the other hand, valve size of natural specimens is inversely proportional to water temperature (Kamiya, 1988; Cronin et al., 2005). Moreover, shell weight of fully calcified specimens collected in natural environments present the same behaviour as valve size, i.e. the higher the temperature, the lighter the valve is, and valve weight is not related to valve size (data from Palacios-Fest and Dettman, 2001; Decrouy, *unpublished data*).

A large database exists on ostracod trace element contents. These data were at first examined in the frame of palaeoenvironmental studies but provide important constraints on biomineralisation in ostracods. Chivas and co-authors (1983, 1986) showed that both the chitin and the soft parts of the animal are enriched in Mg, Sr, and Ba compared to Ca. In addition, these authors observed that the ostracod magnesium content is extremely high in newly formed shells, and that its relative content decreases during shell growth until a specific weight corresponding to full calcification of the carapace. Actually, ostracod comes very close to precipitating magnesite immediately after moulting (Palacios-Fest and Dettman, 2001). The papers of Wansard and co-authors (1998) and of Holmes and Chivas (2002) present a plot showing the exponential decrease of the partitioning coefficient for Mg (D_{Mg} or K_D[Mg]) with increasing Mg/Ca ratios of water. In other words, the less Mg is present in water, the more the ostracod can take up this element from water, suggesting that the metabolism has a control on Mg content. Spatial distribution of Mg has also been studied by several authors. Gradients in Mg/Ca ratio were observed along cross sections of ostracod valves with higher values at the interior and/or at the exterior of the valve, the inner part of the

valve being relatively depleted in Mg (Cadot et al., 1972; Cronin et al., 2005). Morishita and co-authors (2007) studied in detail the distribution of Mg and Sr in *Neonesidae oligodentata*. They observed that the valves consist off three layers: an internal band, rich in Mg, especially in the marginal region, an external band rich in Mg that disappears at the margin and a middle band mostly depleted in Mg. The authors attributed the higher Mg concentration of the outer band to faster calcite precipitation at the beginning of the valve mineralisation process. Slightly coarser grains of the inner band in the marginal region were attributed to more stable crystallisation during the latter stage. They, therefore, suggested that the outer band forms during the earlier stage of the carapace whereas the middle and inner bands might be formed during the latter stages of carapace formation. This model is somewhat in contradiction with the visual observations of Turpen and Angell in 1971. These authors stated that calcification starts at the margins of the valve and gradually proceeds towards the mid-region where calcification is finally completed. The preferential uptake of magnesium in the early stages of valve mineralisation, its distribution across the valve as well as its preferential uptake of Mg-depleted water but its rejection in Mg-rich water, indicate that Mg is actively controlled by the organism and, above all, suggests that Mg plays a crucial role in the calcification processes of ostracod valves.

3.1. Oxygen Isotope Fractionation

A synthesis of the results for Candonidae, Cyprididae, and Cytheroidea is presented in Figure 5.2. Results from previous studies (Xia et al., 1997; von Grafenstein et al., 1999b; Keatings et al., 2002) are also represented on the respective plots for comparison. There are several points of interest in Figure 5.2:

(1) Comparison between oxygen isotope fractionation factors of ostracods and synthetic calcite, both grown in aqueous solutions, clearly support previous observations that ostracod valves do not crystallise in equilibrium, but are enriched in ^{18}O compared to the inorganic carbonate. Another important point is that the regression lines of the fractionation factors versus temperature obtained for certain species are not parallel with the line for equilibrium calcite. Using a slightly different approach and the expression proposed for inorganic calcite by Friedman and O'Neil (1977), von Grafenstein and co-authors (1999b) observed that, for a given species, the difference between ostracod $\delta^{18}O$ values and inorganic calcite $\delta^{18}O$ values was not temperature dependent. These authors stated that oxygen isotope fractionations between ostracods and water can be described using a constant species-specific 'vital offset' that adds up to the value of inorganic calcite. The present dataset clearly demonstrates that the 'vital offset' increases with lower temperatures of crystallisation. In the present paper, the authors prefer, therefore, the term oxygen isotopic 'vital effect' for the difference in oxygen isotope fractionation between synthetic calcite formed in equilibrium with water and ostracods.

It is important to mention that the equation of Friedman and O'Neil uses a second order ($10^6/T^2$) relationship. The extrapolation of their expression to low temperatures results in a steepening of the slope near 0°C. Thus, the difference between an inorganic calcite precipitate calculated according to Kim and O'Neil (1997) and Friedman and O'Neil (1977) is 0.29 ‰ at 20°C but increases to 0.89‰ at 4 °C. This effect may explain in part why von Grafenstein and co-authors (1999b) did not observe a temperature dependence for the 'vital offsets' they obtained. This also indicated the need to use the equation proposed by Friedman and O'Neil (1977) when 'vital offsets' assessed by von Grafenstein and co-authors (1999b) are used, or correct the 'vital offsets' for the specific temperature when the equation proposed by Kim and O'Neil (1997) is used.

(2) Oxygen isotope fractionation factors are, at first view, quite similar within each family, but vary among the different families. Calcification processes must be equivalent or at least very similar within the same genus, subfamily or even family. Hence, the similitude of oxygen isotope fractionation within a family but dissimilarity between taxonomically distant species suggests that isotopic vital effects are due to different biomineralisation processes.

(3) The lines determined for Candonidae species are mostly parallel to the line of synthetic calcites grown in concentrated Ca^{2+} solutions (15 and 25 mM). Still, the lines determined for Candonidae species present an offset of approximately +1 ‰ in comparison to synthetic calcite that grows in the most concentrated Ca^{2+} solution. In contrast, the lines obtained for Cytheroidea species are mostly parallel to the line of synthetic calcite grown at equilibrium (5 mM), but present a somewhat higher offset in comparison with the latter. Slopes determined for Cyprididae species are also less homogenous. This may be an intermediate state between both extremes. If the causes for slope steepening are the same for synthetic calcite grown in concentrated solutions than those for Candonidae and Cyprididae species, the parallel offsets between the latter and lines obtained for ostracods suggests

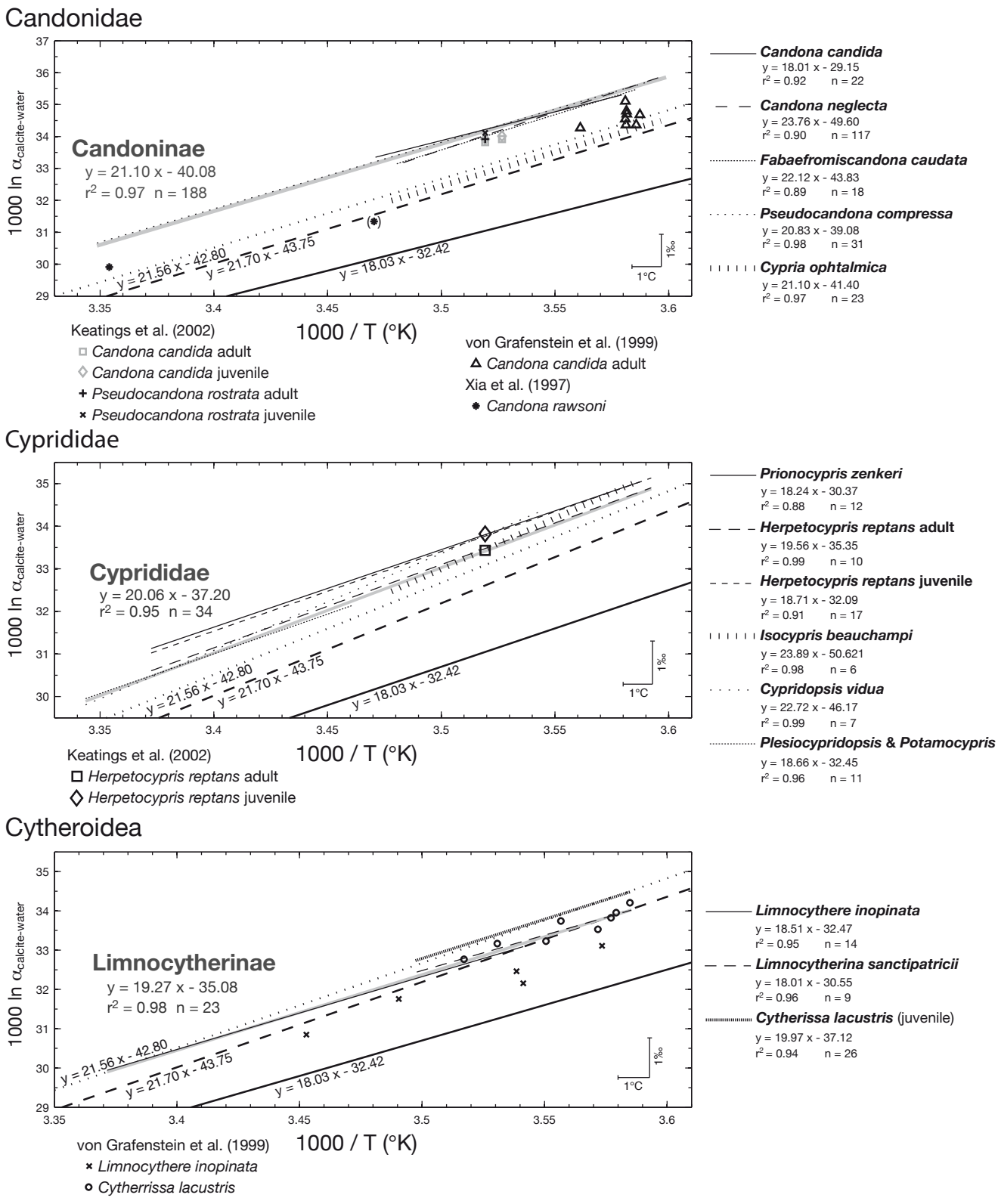


FIGURE 5.2
Oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus 'estimated' valve crystallisation temperatures of adult and juvenile Candonidae, Cyprididae, and Cytheroidea. Ostracod data from von Grafenstein et al., 1999b, Keatings et al., 2002, and present study. Fractionation factors determined by Kim & O'Neil, 1997 of synthetic calcites crystallised from calcium-bearing solutions of 5, 15 and 25 mM (respectively bold, dashed, and dotted line in the lower part of the graph) are also represented in each graph to facilitate comparison.

that isotopic vital effects may be due to two distinct mechanisms. One would be responsible for a non-temperature dependent enrichment in ^{18}O (i.e. a parallel shift of ostracod $10^3 ln\alpha_{calcite\text{-}water}$ toward higher values). The other would be responsible for subsequent slope steepening and additional enrichment in ^{18}O. The first one is referred here as the 'primary isotopic vital effect', whereas the second is referred as the 'secondary isotopic vital effect'. The 'primary effect' may be dominant for Cytheroidea, whereas a combination of both effects is needed to explain the values obtained for Cyprididae and Candonidae. This model further supports the above hypothesis that crystallisation processes are different among taxonomically remote species. It even suggests that a common process, linked to the 'primary effect', is present for at least all species belonging to the Cypridocopina and Cytherocopina infraorder. This basic and fundamental process may, in addition, be reinforced by a second process, linked to the 'secondary effect' in Cypridoidea. This interpretation is supported by differences observed between valve structures of the Cyprididae and Cytheroidea (see below, Keyser and Walter, 2004).

(4) A comparison of the present results with previous ones allows us to test the validity of our approach as well as to test the constancy of vital effects over a broader range of environmental conditions. Oxygen isotope fractionation factors determined by Keatings and co-authors in 2002 for *Candona candida*, *Pseudocandona rostrata*, and *Herpetocypris reptans* species in two small spring-fed ponds in southern England are in agreement with our results. $10^3 ln\alpha_{calcite\text{-}water}$ estimated for *Candona candida*, *Limnocythere inopinata* and *Cytherissa lacustris* collected in the Ammersee and the Starnberger Lakes in southern Germany by von Grafenstein and co-authors (1999b) and *Candona rawsoni* cultivated at 25 °C in vitro by Xia and co-authors (1997) are, in contrast, depleted by approximately 0.75 (≈ 0.75 ‰) in comparison to our results and these of Keatings and co-authors (2002). This discrepancy is even up to one per mil if published 'vital offsets' from von Grafenstein and co-authors (1999b) are used.

pH, or more precisely the relative abundance of bicarbonates ions, can affect oxygen isotope fractionation in foraminifera (Spero et al., 1997; Zeebe, 1999). Different pH may therefore also explain the discrepancy observed for ostracods. Cultures by Xia and co-authors start with a pH of 8.6, the pH of the lakes studied by von Grafenstein and co-authors that range between 7.9 to 8.5, while values for Lake Geneva range between 7.5 and 9, whereas the pH in the ponds studied by Keatings and co-authors have a pH of 6.9 (Xia et al., 1997; Keatings et al., 2002). The lack of a relationship between pH of the different studies and differences in the isotopic vital effects supports the statement already postulated in 2002 by Keatings and co-authors that oxygen isotope fractionation is not affected by the pH of the water. Nevertheless, the chemical composition of water in the different studies is not identical. Water of the Ammersee and the Starnberger See is "hard" water. (Hard water is a water that has high Ca^{2+} and Mg^{2+} content; for $CaCO_3$+$MgCO_3$ lower than 1,4 mmol, water is soft; for values $CaCO_3$+$MgCO_3$ higher than 1.4 mmol, water is slightly hard, very hard water has more than 5.3 mmol $CaCO_3$+$MgCO_3$). Based on the data published in Xia et al. (1997), water used for in-vitro experiments was clearly oversaturated at the beginning of the experiment. Water in the ponds of southern England is, in contrast, clearly under-saturated with respect to calcite (Keatings et al., 2002). Water of Lake Geneva is considered as relative soft water with calcite being under- to slightly-saturated. These observations suggest that vital effects may depend on the degree of calcite saturation: the lower the calcite saturation, the higher the isotopic vital effect is. More generally, the isotopic vital effect may depend of water chemistry and may vary therefore from one site to the other or through time. Further studies, such as for example, ostracods bred in laboratory under different controlled conditions (mainly different pH and chemical composition of water), are essential at this time to determine to which extent vital offsets can vary. Constancy of isotope fractionation is effectively crucial for studies using ostracod valve isotopic composition as palaeoenvironmental proxy.

Concerning the steepness of the slope, a line connecting the value for *Candona rawsoni* at 25°C and the value for *Candona candida* from von Grafenstein et al. (1999b) would be parallel to the one determined for Candoninae in Lake Geneva. In addition, the values for *Limnocythere inopinata* as well as those for *Cytherissa lacustris* determined by von Grafenstein and co-authors (1999b) also seem to be parallel those obtained in Lake Geneva. Parallelism between these lines suggests that chemical composition of water may influence the vital effect, but it is not temperature dependent. Hence, it is possible that chemical composition of water affects the 'primary' isotopic vital effect but not the 'secondary' one.

Last but not least, results presented here do not cast doubts over the validity of the previous studies. Oxygen isotopic compositions of ostracods have proven to reliably reflect oxygen isotope composition of water in continental as well as marine environments (von Grafenstein et al., 2002; Holmes and Chivas,

2002). The present study reinforced the reliability of ostracods as a proxy for past water oxygen isotope compositions. In addition, the present results put further constrains on the temperature dependency of oxygen isotope fractionation in ostracods. Accordingly, a variation of 1 ‰ equals a change of ~4°C for Cytheroidea, whereas the same change in oxygen isotope composition reflects a change of only ~3°C for Candonidae.

4.3. Carbon Isotope Compositions

Because of the reasons mentioned in subsection 3.2, it is difficult to demonstrate that the carbon isotope composition of ostracods is in equilibrium with that of the DIC of water, and, if not, to assess the vital effect for carbon isotope fractionation. Von Grafenstein and co-authors (1999b) observed an enrichment of approximately 1 ‰ between $\delta^{13}C_{ostra}$ and $\delta^{13}C_{DIC}$ values. This enrichment corresponds to the carbon isotope enrichment between calcite and HCO_3^-. This suggests that the carbon isotopic composition of Candoninae is in equilibrium with water DIC. However, other species, such as *Cytherissa lacustris* or *Limnocythere inopinata* have $\delta^{13}C$ values that are much lower compared to the Candoninae. Von Grafenstein and co-workers attributed these relative depletions in ^{13}C to variation of $\delta^{13}C_{DIC}$ values in interstitial water for the former species or vital effects for the second ones. It is stated as a conclusion that a better quantification of variation of pore-water $\delta^{13}C_{DIC}$ and a better definition of species-specific micro-habitats would be necessary to validate or invalidate their hypothesis (von Grafenstein et al., 1999b). Keating and co-authors (2002), using a slightly different method to calculate the expected carbon isotope composition of an "equilibrium" calcite, confirmed that ostracod valves are generally in equilibrium with DIC. Results obtained in lakes (von Grafenstein et al., 1999b, present study) are difficult to interpret because $\delta^{13}C_{DIC}$ values in littoral zones experience large seasonal variations. Moreover, ostracods living in the profundal zones of lakes are mostly infaunal and variations of interstitial pore water $\delta^{13}C_{DIC}$ values can affect geochemistry of the valves. To remedy these complications, micro-habitat preferences as well as life-cycles have been studied in detail here (*Chapter III-2 and IV*).

In term of space and readability, results are not discussed for each species. Equivalent autoecological characteristics are grouped. Two main groups emerge from Figure 5.3. The first one consists of epifaunal forms found in the littoral zones. The second one consists of infaunal forms of the profundal zones. Factors controlling the $\delta^{13}C_{DIC}$ values in ostracod microhabitats were already discussed in *Chapter IV* of the present thesis. The present discussion focuses more on the carbon isotope fractionation, influence of species-specific autoecology, and eventual isotopic vital effects.

Results of the first group are discussed in the following paragraphs. According to the $\delta^{13}C_{DIC}$ results, most of the species living in the littoral zone belong to the Cyprididae and are epifaunal forms (*Prionocypris zenkeri*, *Cypridopsis vidua*, *Plesiocypridopsis newtoni*, *Potamocypris similis*, and *Potamocypris smaragdina*). Some Cyprididae can be found down to the sublittoral zones (*Herpetocypris reptans* and *Isocypris beauchampi*). Some species belonging to Candoninae (*Candona candida*, *Fabaeformiscandona caudata*) and Cytheroidea (*Limnocytherina sanctipatricii*) apparently live in the most superficial sediment and are particularly well adapted to the sublittoral zones. Only one species belonging to the Candoninae is a 'true' littoral form (*Pseudocandona compressa*) whereas one Cytheroidea species (*Limnocythere inopinata*) is a littoral form but can be found in the sublittoral zone. For all these species, a more or less well-expressed negative correlation between $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values was found (*Appendix I*). This indicates that $\delta^{13}C_{ostra}$ values are higher at high temperature and suggests that $\delta^{13}C_{ostra}$ values reflect the seasonality of ^{13}C values of supernatant water DIC

Specimens belonging to *Herpetocypris reptans* and inhabiting the littoral zones as well as specimens belonging to *Cypridopsis vidua*, *Plesiocypridopsis newtoni*, *Potamocypris similis*, and *Potamocypris smaragdina* have all crystallised during the warm period. Besides, most specimens belonging to *Prionocypris zenkeri* were collected during warm periods. For all these specimens, $\delta^{13}C$ values correspond to a value expected for an equilibrium calcite ($\delta^{13}C_{CaCO3}$) that crystallised during the warmest month of the year (large circles on Figure 5.3). This suggests that the valves of these species crystallised in equilibrium with DIC.

Limnocythere inopinata is also a summer form. However, specimens belonging to this species present values that are approximately 2 to 3 ‰ lower than species discussed just above at 2 and 5 m water depth. At these depths, *Limnocythere inopinata* $\delta^{13}C_{ostra}$ values actually correspond to winter $\delta^{13}C_{CaCO3}$ values. At 13 m water depth, values for this species are equivalent to the ones of *Limnocytherina sanctipatricii*. At this depth, $\delta^{13}C_{ostra}$ values of both species are lower by 2 to 3 ‰

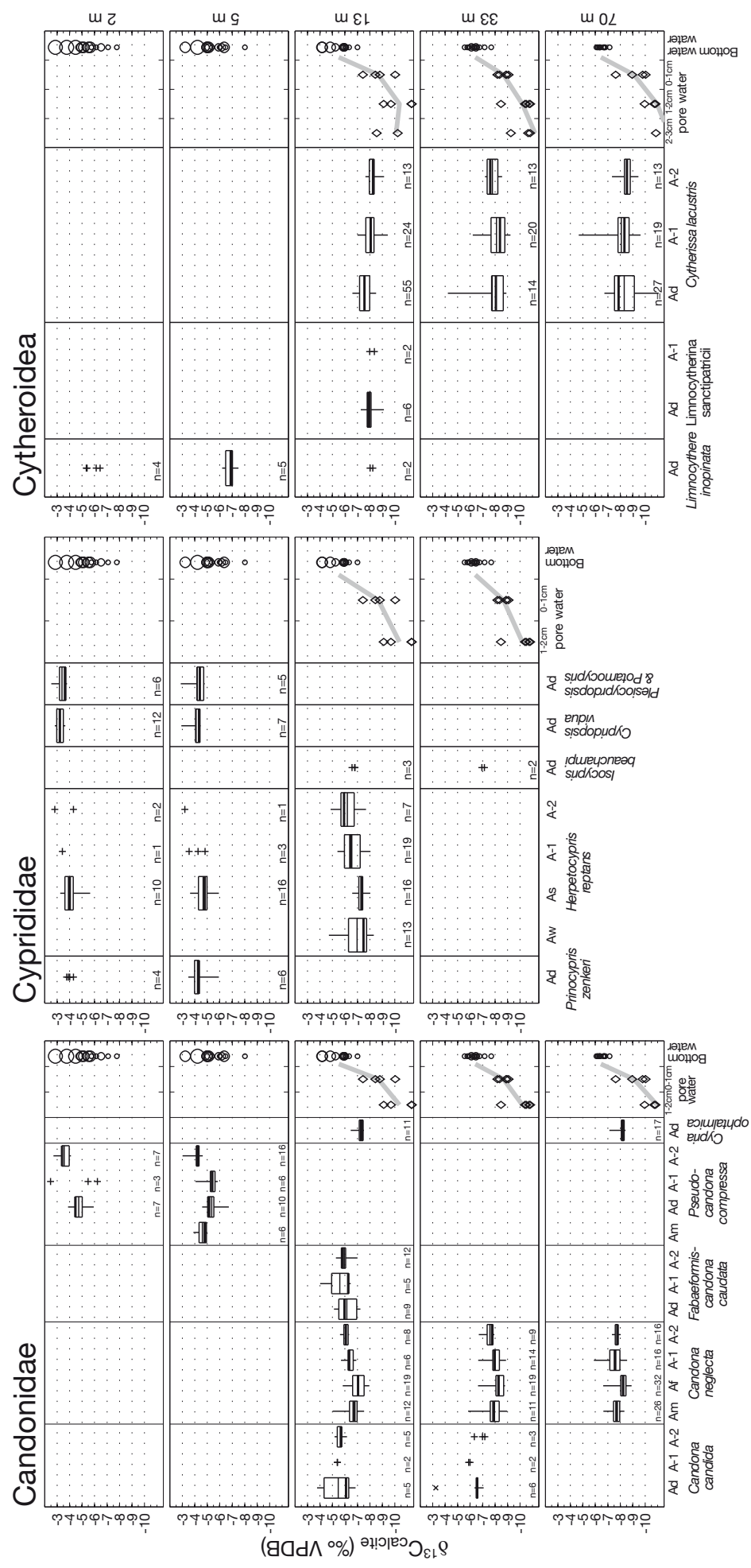


FIGURE 5.3
Carbon isotope composition of Candonidae, Cypridae, and Cytheroidea at 2, 5, 13, 33, and 70 m water depths represented with box plots (minimal value, 1st quartile, median (bold line), average (fine line), 3rd quartile, and maximal value). Crosses are used when samples abundance is low or for outliers. n stand for the number of analyses, Ad for adult valves, Af for female adult valves, Am for male adult valves, A-1 for valves belonging to the last juvenile stage A-1, A-2 for valves belonging to penultimate juveniles stage A-2, Aw and As stand for adult belonging to *Herpetocypris reptans* that crystallised in winter and summer, respectively. Carbon isotope compositions of a calcite in equilibrium with DIC is represented on the right side of each graph to allow for a comparison. Open circles represent the values of a calcite that crystallised in bottom water, marker size being proportional to water temperature at the time of sampling. Open diamonds represent values of a calcite that crystallised in pore water of the top two centimetres of sediment. Grey lines illustrate the average along sediment depth profiles (see text for explanation).

by comparison with values of other epifaunal forms, such as *Candona candida* or *Fabaeformiscandona caudata*. These low $\delta^{13}C_{ostra}$ values correspond to the $\delta^{13}C_{CaCO3}$ values of calcite crystallised in the top centimetres of the sediment. Depletion in ^{13}C for *Limnocythere inopinata* valves was also observed in the Ammersee and the Starnbergersee, where the $\delta^{13}C$ values for this species were even lower compared to $\delta^{13}C$ values of DIC (von Grafenstein et al., 1999b). An infaunal habitat with high penetration depth in the sediment where $\delta^{13}C_{DIC}$ values are lower is not likely because some specimens used for the analyses were recovered on pebbles at 3 m water depth. In addition, examination of specimen sediment penetration depth indicates that both species prefer superficial habitats (*Chapter III-2*). It is concluded that the species belonging to the subfamily Limnocytherinae present a carbon isotopic vital effect with a relative depletion in ^{13}C compared to equilibrium fractionations between calcite and DIC.

Specimens belonging to *Candona candida* and *Fabaeformiscandona caudata* reach maturity in winter. $\delta^{13}C_{ostra}$ values are similar for all development stages examined. These values correspond to $\delta^{13}C_{CaCO3}$ values of calcite crystallised during coldest months. This suggests that valves of both species crystallise in equilibrium with water DIC.

Interpretations of carbon isotope composition of *Pseudocandona compressa* are somewhat more complicated. This species presents different $\delta^{13}C$ values between juvenile specimens and adults. Life-cycle of this species implies that A-2 specimens moult from June to September, i.e. when $\delta^{13}C$ values are the highest. The ostracods overwinter and resume their development as water temperature increases. This development pattern is faithfully reflected in measured $\delta^{13}C_{ostra}$ values. Younger specimen $\delta^{13}C_{ostra}$ values equal summer $\delta^{13}C_{CaCO3}$ values, whereas the increase of $\delta^{13}C_{ostra}$ values from A-1 to adult reflects increase of $\delta^{13}C_{DIC}$ values, and therefore of $\delta^{13}C_{CaCO3}$ values, from winter to summer.

Adult specimens of *Isocypris beauchampi* were recovered at the end of winter and spring, which is in agreement with their measured $\delta^{13}C$ values. This suggests that valves of this species also crystallise in equilibrium with water DIC.

(2) Based on autoecological data and $\delta^{13}C_{ostra}$ values, two species present clearly infaunal behaviour: *Candona neglecta* and *Cytherissa lacustris*. For both species, $\delta^{13}C_{ostra}$ values are not expected to vary seasonally but must, in contrast, reflect the interstitial water $\delta^{13}C_{DIC}$ values with respect to the specific sediment penetration depth of each specimen. For both species, $\delta^{13}C_{ostra}$ values present a high variability and no correlation with $\delta^{18}O_{ostra}$ values (*Appendix I*). This supports the assumption that for these species, $\delta^{13}C_{ostra}$ values reflect $\delta^{13}C_{DIC}$ values of interstitial pore water as well as the high compositional variability found in sediment pore water (*Chapter IV*).

Figure 5.3 illustrates that for these species $\delta^{13}C_{ostra}$ values decrease with increasing water depth. Adults of *Candona neglecta* were mainly found in the first top centimetre of the sediment at 13 m water depth, between 0.5 and 1.5 cm at 33 m water depth and between 1 and 2 cm at 70 m water depth. Adults of *Cytherissa lacustris* were mainly found in the first top centimetre at the three water depths. Specimen abundance found between 0.5 and 1 cm increases with water depth at the expense of specimen abundance in top half centimetre (*Chapter III-2*). This increase of penetration depth with water depth found for both species was related to changes of sediment texture with water depth. The sediment becomes effectively softer with increasing water depth (*Chapter III-2*), which permits the ostracods to dig deeper. $\delta^{13}C_{ostra}$ values faithfully reflect the specimen distribution described above. The decreasing of $\delta^{13}C_{ostra}$ values with increasing water depth may also reflect variations in the rate of decrease of $\delta^{13}C_{DIC}$ values along sediment depth profile. Effectively, the rate of decrease of $\delta^{13}C_{DIC}$ values along sediment depth profiles increases with water depth. In other words, $\delta^{13}C_{DIC}$ profiles are steeper in deep sites. The rate of $\delta^{13}C_{DIC}$ decrease along sediment depth was linked to lower oxygen concentration in supernatant water and higher amount of organic matter in the sediment (*Chapter IV*).

Figure 5.3 also shows that $\delta^{13}C_{ostra}$ values increase with increasing development stage for *Candona neglecta*; whereas the opposite pattern is observed in *Cytherissa lacustris*, i.e. $\delta^{13}C_{ostra}$ values of juveniles are higher than $\delta^{13}C_{ostra}$ values of adults. These differences between $\delta^{13}C_{ostra}$ values can be related to different penetration depths of the different development stages. For *Candona neglecta*, sediment penetration depth increases clearly from the A-4 juvenile stage to adults (*Chapter III-2*, *Appendix I*). For *Cytherissa lacustris*, the trend is less clear. Studies from the Mondsee indicate that adults of *Cytherissa lacustris* dig deeper into the sediment than juveniles (Geiger et al., 1990a; Danielopol et al., 1988). The ability of adults belonging to this species to dig deeper than juveniles was confirmed for ostracods from Lake Geneva. The dataset also suggests that even if the specimens that are found the deepest within the sediment are adults, the general distribution of specimens tends to show a decrease of penetration depth with increasing

development stage (*Chapter III-2*, *Appendix I*). $\delta^{13}C_{ostra}$ values support these observations. $\delta^{13}C$ values of *Cytherissa lacustris* collected in Lakes Ammersee and the Starnberger See show the same increase with age (von Grafenstein et al., 1999b). The authors of this study, based on the results of Danielopol et al. (1988), attributed these higher $\delta^{13}C_{ostra}$ values for adults to deeper habitats. Their reasoning is that in deep sediments, $^{13}C_{DIC}$ values are higher because of the release of CO_2 enriched in ^{13}C produced during methanogenesis. Such an explication is not applicable for Lake Geneva for different reasons. The first one is that, although methanogenesis was detected between 3 and 5 cm in the sediment at 70 m water depth (*Chapter IV*), almost no ostracods live at these depths (*Chapter III-2*). Secondly, the increase in $\delta^{13}C_{ostra}$ values with age is well expressed at 13 m water depth despite the fact that no methanogenesis was detected in the five top centimetres of sediment at this site. Thirdly, autoecological data suggest a slightly deeper habitat for juveniles than for adults, in agreement with the $\delta^{13}C$ values.

Methanogenesis is often used to explain unusual $\delta^{13}C_{ostra}$ values or unexpected trends in $\delta^{13}C$ values. For example, Filippi and co-authors (1999) used the onset of methanogenesis and subsequent release of ^{13}C enriched CO_2 to explain the abrupt increase of $\delta^{13}C_{ostra}$ values they observed during the 20th century in Lake Neuchâtel. Schwalb (2003), in contrast, used methanogenesis to explain a decrease of ostracod $\delta^{13}C$ values. Her reasoning is the following. Seasonal onset of methanogenesis in deeper sediments produces ^{13}C depleted CH_4. As CH_4 diffuses into pore space, it is oxidised by bacterial activity. This produces ^{13}C depleted CO_2 that is added to water DIC leading finally to a decrease of $\delta^{13}C_{ostra}$ values. In the present study, methanogenesis was not observed to affect the $\delta^{13}C_{ostra}$ values although methanogenesis was observed in the deepest sediments at 70 m water depth.

Autoecological and carbon isotopic compositions of the specimens belonging to *Herpetocypris reptans* collected at 13 m water depth present surprising results. This species is mostly regarded as being epifaunal or even phytophylous (Benzie, 1989). While results at 2 and 5 m are in agreement with calcification in open water during summer, it appears that this species develops quite a different behaviour in deeper sites. At 13 m, two generations are produced per year, a summer one and a winter one. Morphological, penetration depth, and oxygen isotopic data suggest that the two generations have quite different microhabitat preferences (*Appendix I*). During winter, A-1 and adult specimens were largely found in the very topmost sediments. Isotopic analyses reveal a negative relationship between $\delta^{18}O$ and $\delta^{13}C$ values, suggesting that the ostracods recorded $\delta^{13}C_{DIC}$ values of supernatant water. A-1 and adult specimens belonging to the summer generation were, in contrast, found deeper in the sediment. Their $\delta^{13}C_{ostra}$ values are low in comparison with values expected for a calcite crystallised during summer and values show only low variability. This suggests that the animals calcified their valves in a relatively deep and chemically homogeneous microhabitat. Hence, the difference between $\delta^{13}C_{ostra}$ values of summer and winter adults is due to a seasonal change of microhabitat preferences. The decrease of $\delta^{13}C_{ostra}$ values with age is simply interpreted as representing increasing depth of habitat with age like in other species.

Given that adults of the winter generation record $\delta^{13}C_{DIC}$ values of supernatant water and that A-2 specimens have a superficial micro-habitat, the measured $\delta^{13}C_{ostra}$ values for *Herpetocypris reptans* seem to be too low compared to the values expected for equilibrium growth of calcite from DIC. Keatings and co-authors (2002) also observed a depletion of 0.8 ‰ compared to equilibrium values for a synthetic calcite. These observations point towards a slight negative isotopic vital effect for this species.

Cypria ophtalmica is also believed to be an epifaunal and/or phytophylous form (Hiller, 1972). Autoecological and carbon isotopic data suggest that in lakes, this species inhabits the interstices of the sediment. The rather scarce autoecological data obtained so far may hint at a more superficial habitat. If this is correct, this species would present a quite significant negative vital effect for carbon isotopes.

It is of interest to note that the species possessing rather thin and weakly calcified valves, such as Limnocytherinae or *Cypria ophtalmica*, present a negative vital effect for carbon isotopes. The carapace of the latter species consists mainly of amorphous material that, in other well-calcified species, is recrystallised at a later stage (Keyser and Walter, 2004). The amorphous calcium carbonate may be in disequilibrium during early stage of valve calcification. Due to recrystallisation during final calcification, disequilibrium $\delta^{13}C$ values may be erased. And this signal would only be preserved in species that do not finalise the calcification process (see also following subsection 4.4).

4.4. Effect of Incomplete Valve Calcification

Xia and co-authors (1997) observed that the ostracods they bred at 15 °C were less calcified (lower shell weight) and had much lower oxygen isotope fractionation factors than expected for equilibrium growth of calcite (symbol in brackets in Figure 5.2). In addition, development and survival rates were much lower at 15°C than at 25°C. Optimum life temperatures for *Candona rawsoni* is 25 °C. The authors thus interpreted the relatively depleted oxygen isotopic compositions and the lower shell calcification as being due to experiment stressful conditions. The authors attributed lower fractionations of O-isotopes at 15 °C to slower calcification processes. In general, rapid precipitation of carbonate in organisms such as corals is expected to discriminate less between ^{16}O and ^{18}O, leading to lower $\delta^{18}O$ values compared to equilibrium values (McConnaughey, 1989). A decrease of $\delta^{18}O$ values with increasing precipitation rate has also been observed in synthetic carbonate minerals (Kim et al., 2006). Xia and co-authors (1997), noted the discrepancy between their hypothesis and the general behaviour observed for fast calcifying carbonates. Actually, there is no evidence that the crystals secreted by the organism grows slower at 15 °C, than at 25 °C.

During the one-year sampling in Lake Geneva, some ostracod specimens were only partially calcified. In our case, incomplete calcification of the valve was attributed to the fact that these specimens were sampled just after ecdysis and were killed before complete valve calcification. Once the soft tissue is chemically eliminated, such incompletely calcified valves are easily recognised. Most of them are too fragile and break even during cleaning and picking with a fine pencil brush. These valves were discarded. Those that did not break during handling were retained but for adults and A-1 juveniles, the low shell weight readily permitted detection of incompletely calcified valves. These valves were regrouped and analysed separately. $\delta^{18}O$ values for these samples did not have any inconsistency with values of other samples. However, these samples often have $\delta^{13}C$ values of 1 to 3 ‰ higher than normally calcified valves. For example, the carapace having the highest $\delta^{13}C_{ostra}$ values found for adult *Candona candida* at 33 m (outlier value symbolised with the cross in Figure 5.3) had the weight of only 1/4 of the typical weights of the species. Thus, incomplete valve calcification has an effect on the stable isotope composition: $\delta^{13}C$ values are higher in Lake Geneva, whereas Xia and co-workers (1997) found lower $\delta^{18}O$ values compared to the bulk populations.

The crystallisation site in ostracods can been envisaged as occurring from a solution separated from the external environment by organic membranes (see also *Chapter I*). Chemical Equilibrium between both internal solution and lake water must occur through this membrane or via body fluids of the ostracod. This mechanism might, in addition, be 'biologically' controlled. Thus, the internal solution can be seen as a finite reservoir of DIC that has to be continuously refilled via permeability of the organic membranes and/or substances secreted by epidermal cells. Knowledge on mineralisation processes in ostracods is quite limited but a one point is clear: the ostracods have a strong control on the timing of calcification.

Precipitating instantaneously different fractions of witherite ($BaCO_3$) from a finite DIC reservoir, Kim and co-authors (2006) demonstrated that CO_3^{2-} was preferentially incorporated into the growing witherite crystal. As O-isotopic fractionation between water and CO_3^{2-} is lower in comparison to the other DIC species, the isotopic composition of a mineral representing only a small amount of the original DIC reservoir has lower $\delta^{18}O$ values. This phenomenon may explain the oxygen isotope effect observed for incomplete ostracod valve calcification. Before valve calcification, a certain amount of DIC is present in the internal solution. At the beginning of valve calcification, the organism has to induce precipitation of the calcite. This forced precipitation may be comparable to the instantaneous precipitation of synthetic witherite in a finite reservoir. Hence, the first calcite that mineralises, may incorporate a larger proportion of CO_3^{2-}. As calcite is recrystallised at later stages of valve calcification, this isotopic signature of CO_3^{2-} is slowly erased as the DIC pool is being consumed and/or as the carbonate re-equilibrates with water.

Carbon isotope enrichment factor between CO_3^{2-} and HCO_3^- ranges between 2.3 and 3.3 ‰ from 20 to 4 °C (Zhang et al., 1995). Hence, if more CO_3^{2-} is incorporated, the $\delta^{13}C$ value is expected to be higher than equilibrium. Unfortunately, Xia and co-authors (1997) did not present the carbon isotopic composition of their cultured ostracods. However, an enrichment of 1 to 3 ‰ is observed for non-complete calcified valves in the present dataset. This could provide further evidence that CO_3^{2-} is preferentially incorporated during the initial phase of valve calcification.

Homogeneity of the isotope compositions of well-calcified samples implies that the initial calcium carbonate formed at the beginning of valve calcification must re-equilibrate to reach its final constant values.

Once the first calcium carbonate has crystallised, re-equilibration is only possible via re-crystallisation of the minerals. Using SEM microphotographs and EDX-analyses, Keyser and Walter (2004) demonstrated that the ostracod valve calcification process consist of successive precipitation and re-crystallisation of different mineralogical phases. Thus, it is possible that the isotopic signature of preferential CO_3^{2-} uptake is erased during final re-crystallisation. Effects of incomplete valve calcification can, therefore, only be observed in incompletely calcified valves.

The fact that the effect of incomplete valve calcification was observed only for carbon isotope compositions and not for oxygen isotopes in the present study may be due to re-equilibration of oxygen isotopes whereas carbon isotopes remain stable. This may be the case because the pool of oxygen is much larger than the pool of carbon in the solution found in calcification site. This effect of incomplete valve calcification may also be more important in stressful laboratory conditions and affect therefore both carbon and oxygen isotopes, while only carbon is affected in natural environments.

4.5. Biomineralisation Processes Versus Stable Isotope Fractionation – Towards an Understanding of Isotopic Vital Effects in Ostracods

4.5.1. Effect of pH at the crystallisation site

Keatings and co-authors suggested in 2002 that the non-equilibrium fractionation of oxygen isotopes in ostracods as well as carbon isotopic non-equilibrium for *Herpetocypris reptans* might be explained by a fixed pH at the site of calcite crystallisation and controlled by the organism. This interpretation is based on the proposition of Zeebe (1999) that oxygen isotope fractionation is dependant of water pH. According to Zeebe (1999): "The different hydrate carbonate species can be expressed with $S = [H_2CO_3] + [HCO_3^-] + [CO_3^{2-}]$ and the relative proportion of these carbonate species is function of the pH. Provided that calcium carbonate is formed from a mixture of the carbonate species in proportion to their relative contribution to S, the oxygen isotope fractionation factor between calcium carbonate will reflect the balance between the different oxygen isotope fractionation factor between the different carbonate species and water according to their relative proportion to S. As oxygen isotope fractionation factors between the different carbonate species and water decrease according to the sequence $\alpha_{H2CO3-water} > \alpha_{HCO3-water} > \alpha_{CO3-water}$, and as increasing pH lead to the deprotonation sequence $[H_2CO_3] \rightarrow [HCO_3^-] \rightarrow [CO_3^{2-}]$, the $\delta^{18}O$ value of calcium carbonate decreases with increasing pH". Under this assumption, Zeebe (1999) attributed the non-equilibrium fractionation factor obtained by Kim and O'Neil (1997) in 15 and 25 mM Ca^{2+} solution to precipitation at lower pH. To confirm his model, Zeebe (1999) recalculated the pH during calcite precipitation and found that pH of the solution at the time of crystallisation must have been 6.9 and 6.6 for 15 and 25 mM Ca^{2+} solutions, respectively. The similarity between oxygen isotope fractionations of ostracods and synthetic calcite precipitated in 25 mM Ca^{2+} solution lead Keatings and co-authors (2002) to suggest that pH at the site of calcite precipitation in ostracod may be relatively low (≤ 7) and is responsible for the oxygen isotope vital effect.

Seven years after the proposition of Zeebe, Kim and co-authors (2006) proved experimentally that oxygen isotope fractionation for calcium carbonate that precipitates under equilibrium is not pH dependent. This was actually postulated theoretically by Deines in 2005. These results suggest that pH at the calcification site is not able to explain the enrichment in ^{18}O observed in ostracod valves. Studying pH in the cuticle during the different moulting stages might be very informative on ostracod biomineralisation and help to discard or prove an effect of pH on isotopic fractionation.

4.5.2. Effect of calcification rate

Von Grafenstein and co-authors noted in 1999b that species having the shortest instar development have higher $\delta^{18}O$ values than species developing slowly. On the base of this observation, these authors suggested that the differences of oxygen isotope fractionations observed among the different species might be correlated to the speed of valve calcification. Our dataset for Lake Geneva clearly indicates that their initial observations are not valid in this case. For example, *Candona neglecta* develops rather slowly and continuously at 70 m water depth but grows by steps at 13 m with a long summer period of latency and fast development when environmental conditions are favourable. In spite of these different developments, their oxygen isotope fractionations are equivalent for *C. neglecta* in all sites. Another observation supporting that development rate have no influence on isotopic fractionation is that both *Limnocythere inopinata* and *Limnocytherina sanctipatricii* have lower $10^3 \ln\alpha_{calcite-water}$ even though both species develop particularly rapidly (for species development, see *Chapter III-2*).

However, speed of calcite growth may not at all be related to instar development speed. As long as the true calcification rate is not known, it is not possible to demonstrate if rapidity of valve calcification process

affects the isotopic composition of fully calcified valves. As discussed above, kinetic effects linked to forced calcification during initial valve calcification stage may affect the isotopic compositions of valves of non-completely calcified valves but, if this is true, this effect is erased during the later valve calcification stage.

4.5.3. Deprotonation of HCO_3^- as source of CO_3^{2-}

As discussed above, the crystallisation site may be seen as a closed system. Depending on the pH, carbonate ions available for carbonate mineralisation in the internal solutions are H_2CO_3, HCO_3^-, and CO_3^{2-}. CO_3^{2-} is the first carbonate ion to precipitate, whereas HCO_3^- and H_2CO_3 must at first be deprotonated before being added to the mineral. The amount of DIC present in the internal solution before crystallisation as calcite is certainly not sufficient to provide bicarbonate for calcification of the whole shell. Transfer of DIC from lake water towards the internal solution is therefore necessary for a complete valve calcification. If mass transport is rapid, i.e. faster than DIC is consumed for calcite precipitation, and if carbonate species are neither chemically nor isotopically fractionated during incorporation and transfer to the calcification site, and if calcite precipitation is slow, i.e. no kinetic fractionation occurs during calcite precipitation, then the calcite precipitated must be in equilibrium with surrounding water. In natural water, the main carbonate species present in water is HCO_3^-. Thus, it is plausible that the main species present in the calcification site is HCO_3^-. Under instantaneous precipitation of synthetic calcium carbonate in a closed system, the ions incorporated in the minerals preserve their original isotopic composition. At a high pH, the first carbonates that crystallised have $\delta^{18}O$ values that reflect the isotopic fractionation between CO_3^{2-} and water. In contrast, calcium carbonate issued from the instantaneous precipitation of all the DIC at neutral pH have $\delta^{18}O$ values that tend toward isotopic fractionation between HCO_3^- and water (Kim et al., 2006). As $\alpha_{HCO3\text{-}water}$ is higher than $\alpha_{calcite\text{-}water}$, $\delta^{18}O$ value of an instantaneously formed calcite precipitated from a large proportion of the available DIC pool in a closed system is higher than equilibrium calcite $\delta^{18}O$ value.

In the case of the ostracods, if mass transport from lake water to their internal body fluid is not sufficiently rapid in comparison with calcite precipitation, calcite precipitation occurs via deprotonation of HCO_3^-. As deprotonation occurs very quickly, the newly formed CO_3^{2-} ions will preserve the isotopic composition of HCO_3^- from which they originate, leading to an enrichment in ^{18}O of ostracod valves.

Another case could be that that mass transport is rapid enough but there is a preferential uptake of HCO_3^- during transport of DIC from lake water to body fluid. In this case, calcification also occurs via a deprotonation of HCO_3^- and immediate incorporation of CO_3^{2-} ions into the crystal lattice that have preserved the initial isotopic composition of HCO_3^- ions. This leads to the same increase in ostracod calcite $\delta^{18}O$ values. To date there are no data that supports that calcification sites in ostracods are separated from the external environment. Selective integration of chemical compounds in ostracods has also not been investigated up to now. Better knowledge, especially on the body fluid composition and transfer during valve calcification, are needed to support or reject the hypothesis that precipitation is fast and occurs in a finite reservoir, which is not in equilibrium with the surrounding water. Still, until now, no process was able to explain the enrichment in ^{18}O of ostracod calcite. Integration of deprotonated HCO_3^- ions that has preserved their initial oxygen isotopic composition is one of the few possible processes that can explain the preferential incorporation of ^{18}O in ostracod valves.

4.5.4. Salt effect

As stated above, oxygen isotope fractionation factors determined for ostracods are very similar in terms of temperature dependence (slope steepness) and offset from equilibrium to the one determined by Kim and O'Neil in 1997 for synthetic calcite precipitated in highly concentrated Ca^{2+} solutions. These authors suggested that precipitation in concentrated solution was not at equilibrium but did not discuss further the mechanism that might account for this non-equilibrium. Moreover, the authors point out that the non-equilibrium fractionation factors they obtained might reflect some "equilibrium system not yet identified". Ten years later, Kim and co-authors (2007) observed that high concentration of Mg^{2+} have an effect on oxygen isotope fractionation and associated their observations to the salt effect.

Many studies demonstrated that the isotopic composition of CO_2 in equilibrium with highly concentrated solution (*activity*-ratio) has lower $\delta^{18}O$ value than the water before addition of the salts (*composition*-ratio) (O'Neil and Truesdell, 1991; Horita et al., 1993a, b). *Activity*-ratio refers to the oxygen isotopic composition of CO_2 in equilibrium with the salt solution; *Composition*-ratio refers of to the oxygen isotope of the water before adding salt. O'Neil and Truesdell (1991) proposed two mechanisms to explain this phenomenon when the isotopic composition of water is determined by the CO_2-H_2O equilibration technique: (1) fractionation

among the three oxygen-bearing species (bound or solvation water, free water, and CO_2) in the system, and (2) modification of the structure of water in the presence of ions. It can be inferred from the first mechanism that Mg^{2+} ions, being structure-makers, will preferentially attract ^{18}O-rich water molecules to their hydration spheres, leaving the free water proportionally enriched in ^{16}O. Therefore, a mineral precipitating from such a solution is expected to be in equilibrium with the free water and, when fractionation factors are calculated on the basis of the isotope *activity*-ratio, results shall be identical to dilute systems. Kim and co-authors (2007) observed a positive shift of 0.4 ‰ for aragonite precipitated in highly Mg^{2+} concentrated solutions when fractionation factor are calculated on the basis of the isotope *activity*-ratio. To explain this discrepancy, they suggested that whether (1) the isotopic activity composition of concentrated solutions determined by the CO_2-H_2O equilibration technique does not reflect the true isotope activity ratios of concentrated solution or (2) the presence of high concentrations of Mg^{2+} ions modifies the mechanism(s) of aragonite precipitation and results in its relative enrichment in ^{18}O.

The mechanism(s) of oxygen isotope salt effects in mineral-water systems remains unclear. Still, high salt content has an evident effect on oxygen isotope fractionation in carbonate-water system. Effect of salt concentrations on $\delta^{18}O$ values of CO_2 in equilibrium (O'Neil and Truesdell, 1991) might help to understand non-equilibrium observed in ostracods. O'Neil and Truesdell (1991) observed that the salt effect is higher for strong structure-making ions than for relatively weaker structure-making ions. Importance of the salt effect follows the sequence $Al^{+3} > Mg^{2+} > Ca^{2+}$. In addition, the authors showed that salt effect increases with decreasing water temperature. The slope is identical for the different structure-making ions. The slopes determined for different concentrations of solution of the same salt are parallel but, at a critical concentration, which varies for each salt, the slope of the lines changes to be steeper. These observations present several similarities with the results of Kim and O'Neil (1997) and the present study. For the three systems (CO_2-'salt enriched solution', calcite-'Ca^{2+} enriched solution', and ostracod-water), the lines determined present a positive offset from equilibrium (i.e. lower salt content for CO_2 and calcite). These lines present steeper slopes than the line for equilibrium. Within a single system, the lines are parallel, however, at a certain critical Ca^{2+} concentration, or between Cytheroidea and Cypridoidea, slopes change to be steeper (see differences between Cyprididae and Candoninae in Figure 5.2). These similarities suggest that non-equilibrium observed for synthetic calcite precipitated in Ca^{2+} concentrated solution is due to the change of water structure due to the addition of salt. As Ca^{2+} ions are structure-making, the $\delta^{18}O$ value of the hydration spheres is believed to be higher than that of the non-bound water molecule. If this is correct, oxygen isotopes incorporated and or adsorbed to the surface of the growing mineral may actually be in (partial) equilibrium with water of the hydration spheres. This could happen via equilibration of bicarbonates or carbonates ions with the water of hydration sphere as carbonates ions get closer to the growing mineral. This proposition is difficult to prove but may explain the vital effect observed in ostracods. Essentially, Mg^{2+} concentration is high during initial valve calcification (Chivas et al., 1983, 1986; Palacios-Fest and Dettman, 2001). In addition, a large amount of Ca^{2+} is released from epidermal cells into calcification sites at the same stage (Keyser and Walter, 2004). Thus, salt concentrations may be very high in calcification sites at the beginning of valve calcification. This may lead, via the salt effect, to the enrichment in ^{18}O observed in ostracod valves. It is difficult to know whether Mg^{2+} or Ca^{2+}, or a combination of both cations, is responsible for the vital offset observed in ostracod valves.

Hence, the different offsets and slopes for fractionation factor found for the different species may be due to relatively different salt concentration in calcification site. If Ca^{2+} is responsible for the isotopic vital effect, abundance of apatitic granules might be linked to a higher isotopic vital effect. On the other hand, if Mg^{2+} is responsible for the isotopic vital effect, it may be expected that vital effect would be higher in organisms presenting higher magnesium partitioning coefficient. First results indicate that, in general, the higher the D_{Mg} is, the lower the vital offset is (*Appendix I*). However, this does not discredit the hypothesis that Mg^{2+} is responsible for the vital effect. Effectively, Mg^{2+} is expected to prevent the formation of calcite (Davis et al., 2000). Therefore, Mg^{2+} might have the role of crystallisation inhibitor during ostracod valve calcification. This would imply that Mg^{2+} has to be evacuated from the calcification site as calcite is precipitated. Hence, even if Mg^{2+} has an important role during valve calcification, its abundance in the fully calcified valves may not be representative of Mg^{2+} concentration in the first stage of valve calcification. A visual inspection of carapace structures with parallel isotopic and trace element content analyses made at different moulting phases for different species may permit to elucidate the cause of isotopic vital effects in ostracods. In parallel, a comprehensive understanding of all factors implied in inorganic carbonate precipitation is necessary to understand the reasons of vital effects present in ostracods as well as in many other taxa.

5. Conclusions

Studies of stable isotope compositions of living ostracods collected in a natural environment during a year at one-month intervals permitted to produce a large database. Studies made in parallel on ostracod autoecology and environmental parameters allows for the determination of oxygen isotope fractionation factors for ostracods and to test whether carbon isotope composition of ostracod valves are in equilibrium with the DIC of water or not. The results show that:

(1) Oxygen isotope fractionation is equivalent for all species belonging to Candoninae and leads to an enrichment in ^{18}O of more than 3 ‰ relative to equilibrium values estimated for inorganic calcite. Oxygen isotope fractionation for the species presents the same dependency to temperature than synthetic calcite precipitated in Ca^{2+} concentrated solutions (Kim and O'Neil, 1997). Oxygen isotope fractionation for Cytheroidea is less discriminative relative to the oxygen isotopes, with enrichments in ^{18}O for these species being 1.7 to 2.3 ‰. Oxygen isotope fractionation for theses species presents the same temperature dependency than equilibrium calcite. Oxygen isotope fractionations determined for Cyprididae plot in-between the results of the two previously cited Families. The difference in oxygen isotope fractionation between ostracods and inorganic calcite has been interpreted as resulting from a 'vital effect'.

(2) Comparison with previous work suggests that oxygen isotope fractionation might be dependent of the chemical composition of water, with fractionation being lower at higher calcite saturation of the host water.

(3) Carbon isotopic compositions of ostracod valves are generally in equilibrium with DIC. The specimens' $\delta^{13}C_{ostra}$ values are mainly controlled by seasonal variations of $\delta^{13}C_{DIC}$ or variation of $\delta^{13}C_{DIC}$ in sediment pore water. Species having thin valves (*Cypria ophtalmica*, *Limnocythere inopinata*, and *Limnocytherina sanctipatricii*) have $\delta^{13}C_{ostra}$ values that are lower in comparison with inorganic calcite in equilibrium with DIC. This relative enrichment in ^{12}C has been interpreted as resulting from a 'vital effect'.

(4) Incomplete valve calcification has an effect on the carbon and oxygen isotope composition of ostracod valves. Preferential incorporation of CO_3^{2-} at the beginning of valve calcification may explain this effect. The isotopic composition of first minerals that crystallised is erased as the valves recrystallise during late stages of calcification.

(5) Results presented here as well as results from synthetic carbonate experiments indicate that the different models suggested by previous studies are not able to explain the oxygen isotopic 'vital effect' in ostracods. Two mechanisms that might generate an enrichment in ^{18}O of ostracod valves are proposed. The first mechanism, deprotonation of HCO_3^-, may contribute to valve calcification of all ostracod taxa and is responsible for a non-temperature dependent enrichment in ^{18}O. The second mechanism may be only present in Cypridoidea and would be responsible for additional enrichment in ^{18}O as well as higher temperature dependency of oxygen isotope fractionation.

Chapter V - 2 :

CONTROL ON OSTRACOD VALVE GEOCHEMISTRY: PART II. MG/CA AND SR/CA RATIOS

1. Introduction

Ostracods are small microcrustaceans embedded in a low-Mg calcite shell. Like other crustaceans, ostracods grow by successive moulting (ecdysis). During moulting, the carapace is cast and a new one is calcified within a few hours (Turpen and Angell, 1971) to a few days (Roca and Wansard, 1997). Ostracods are mainly benthic organisms that colonize all aquatic environments. In lakes they occur from the littoral zones down large depths. In addition, ostracod fossils are generally abundant and well-preserved within sediments.

Hence, ostracod valves are potential archives of punctual past environmental conditions. Trace element contents of ostracod valves have proven useful for palaeoenvironmental reconstructions in marine, brackish, and freshwater environments. Mg/Ca ratios of *Krithe* permit, for example, the reconstruction of past changes in ocean bottom water temperatures (Dwyer et al., 1995, 2002). At the continental margins, trace element contents of ostracod valves can be used together with stable isotope composition to distinguish open marine condition, brackish water, or continental influences (De Deckker et al., 1988; Anadón et al., 2002; Janz and Vennemann, 2005). In arid regions or in closed basins, Mg/Ca and Sr/Ca ratios are used to reconstruct past salinity to estimate changes in evaporation/precipitation ratios (Engstrom and Nelson, 1991; Yu et al., 2002; Tütken and Vennemann, 2006). It is possible to separate the effect of water temperature from change in salinity by coupling Mg/Ca and Sr/Ca ratios with oxygen isotope data (Chivas et al., 1993). Ricketts and co-authors (2001) used the uranium content of ostracod valves to assess oxygen content of the deep water. In temperate regions, Mg/Ca ratios of ostracod valves can be used to infer past water temperature (Wansard, 1996; Palacios-Fest et al., 2002).

Success of such studies relies on the availability of modern analogues. Without these, it is not possible to assess how environmental conditions are recorded by the ostracod shell geochemistry. This is especially important when quantitative reconstructions are attempted. Trace element content is considered to change with genus (Holmes and Chivas, 2002). The relation between environmental parameters and the trace element contents of ostracod shells must, therefore, be determined for each species. If this is achieved, quantitative reconstruction can be performed on the basis of ostracod trace element contents. This approach has been undertaken successfully since the eighties. Nevertheless, there still remain discrepancies among different authors despite the large number of studies having examined trace element incorporation in ostracods (e.g. Wansard and Mezquita, 2001; Dettman et al., 2002).

To study the regional variation of climate during global climate change, climatologists need a dense network of reliable palaeoclimatic reconstructions over large regions. If variations of bottom water temperature can be estimated with another method than oxygen isotope composition, it would be possible to correct oxygen isotope composition of ostracod valves for the temperature effect and hence get a reliable record of lake water isotopic composition. This method might also be used in lakes northerly to test if water temperature was constant over the whole period investigated. As trace element contents of bottom water in great lakes are expected to be constant over longer periods, trace element contents of ostracod, especially Mg/Ca ratios, may provide a valuable tool to reconstruct past water temperature.

Many studies demonstrated that trace element uptake depends of the concentration of the elements in water (Chivas et al, 1983, 1986; Wansard et al, 1998; De Deckker et al., 1999). Trace element uptake, especially magnesium, is also temperature dependent (Chivas et al, 1983, 1986; De Deckker et al, 1999; Palacios-Fest and Dettman, 2001; Cronin et al, 2005; Kondo et al, 2005). In some cases, it can be very difficult to distinguish which parameter between water trace element content (Mg/Ca_{H2O} or Sr/Ca_{H2O}) and temperature of water controls the incorporation of the element during ostracod valves calcification (Wansard and Mezquita, 2001; Dettman et al., 2002). This difficulty is due to the positive relationship between trace element content and temperature in a calcite saturated aquatic environment. Effectively, as water

temperature increases, calcite saturation increases and authigenic calcite precipitates. This effect is generally amplified by photosynthesis of macroalgae and macrophytes. Calcite precipitation leads to a depletion of calcium concentration in water. As magnesium and strontium are generally conservative, i.e. they do not precipitate together with calcite, the Mg/Ca and Sr/Ca ratios increase linearly with water temperature. Hence, the Mg/Ca and Sr/Ca ratios of ostracod valves correlate with water temperature and Mg/Ca and Sr/Ca ratio of water. In other words, the effects of both environmental factors cannot be separated. Some authors argue that the Mg/Ca and Sr/Ca ratios of water are the preponderant parameter (Wansard and Mezquita, 2001); whereas others argue that trace element uptake in ostracods depends primarily on the temperature of water (Dettman et al., 2002). It is naturally also likely that both parameters have an effect on Mg/Ca and Sr/Ca ratios of ostracod valves, the one effect adding to the other.

The littoral zones of Lake Geneva present also a relationship between the trace element content of water and temperature. Lake Geneva water is slightly under-saturated to saturated in respect with calcite. Photosynthesis is the major factor triggering calcite precipitation (*Chapter IV*). This interpretation is supported by the linear positive relationships found for Mg/Ca or Sr/Ca ratios of water and $\delta^{13}C_{DIC}$ values as well as temperature. Because water Mg/Ca and Sr/Ca ratios vary concomitantly with water temperature, it will remain to be difficult to distinguish which of these parameters control the trace element uptake during valve calcification. As ostracods develop naturally in their preferential habitat, no stress effects are expected which is in contrast to laboratory experiments where such effects may falsify the results (Engstrom and Nelson, 1991; Xia et al., 1997). In addition, fossil ostracods used for palaeoenvironmental reconstructions have grown in complex environments and not in the laboratory with only one variable changing with time. 'Natural environments' are, therefore, an opportunity to study the end products of the interaction of all environmental controls. Such studies are fundamentals, in addition to laboratory experiments, to grasp how past environmental conditions are recorded in ostracod valves.

The aim of the present study is to test whether magnesium and/or strontium content in ostracod valves can be use as palaeothermometer. To achieve this, trace element contents (magnesium and strontium) of living ostracods from Lake Geneva were analysed and compared to monitored environmental parameters. Our dataset also allows us to evaluate which environmental parameters control ostracod valve geochemistry and to better constrain the use of ostracod valve geochemistry as a palaeoenvironmental proxy.

2. Results

Mg/Ca and Sr/Ca mole ratios were determined for adult and juvenile specimens belonging to 15 species (raw ostracod geochemical data can be found in *Appendix II*). For each sample, oxygen and carbon isotopic compositions are known as isotopic and trace element content analyses were made on the same samples. In addition, water temperature during the valve calcification and moulting period were estimated in a previous study using $\delta^{18}O$ values and species-specific life-cycles (*Chapter III-2* and *V-1*). Microhabitat preferences were also established using specimen sediment penetration depths and $\delta^{13}C$ values (*Chapter V-1*). Concerning environmental parameters, monthly Mg/Ca and Sr/Ca ratios of water were determined for all sites. Compositional variations in sediment pores were also investigated. A detailed examination of the different factors controlling the spatial and temporal variation of environmental parameters is presented in another paper (*Chapter IV*). Hence, the present study has at disposal a very complete, detailed, and unique dataset on ostracod valve geochemistry, species-specific autoecology, and environmental parameters.

Given the large number of samples, results of the different species were regrouped in the two subfamilies Candoninae and Cyprididae and in the superfamily Cytheroidea. Raw Mg/Ca and Sr/Ca results for adults and juveniles of each species are illustrated using histograms in electronic appendixes EA-1, EA-3, and EA-5 for Candoninae and Cyprididae, and Cytheroidea, respectively (electronic appendixes can be found at the end of the present chapter). Geochemistry of the valves is graphically represented in Figures 5.4, 5.5, and 5.6 for the same respective families. In these diagrams, trace element contents (Mg/Ca and Sr/Ca ratios) are plotted against the stable isotope compositions of the valves ($\delta^{13}C$ and $\delta^{18}O$ values) and amongst each other (Mg/Ca vs. Sr/Ca).

For all Mg/Ca and Sr/Ca results, the respective partition coefficients D_{Mg} and D_{Sr} were determined according to the equation:

$$D_X = X/Ca_{ostra} / X/Ca_{H2O} \qquad (5.5)$$

where X/Ca_{ostra} is the molar ratio between the element X and calcium measured on ostracod samples and X/Ca_{H2O} the molar ratio between the element X and calcium measured on monthly water samples. X/Ca_{H2O} can correspond to the values of the date or to the values one or more months preceding sampling according to the estimated time period when the ostracods moult before sampling (= calcification time). This one is at first view unknown but was already assessed for examination of oxygen isotopes fractionation (*Chapter V-1*). X/Ca_{H2O} values used in equation (5.5) were primarily fixed on the basis of these pieces of information and refined using best-fit correlations. Mean partition coefficients for adults are presented in Table 5.2, 5.4, and 5.6 for Candoninae, Cyprididae, and Cytheroidea, respectively. In these tables, the species representing a thermo-dependence of trace element uptake (see below) are labelled with an exponent 't'. Correlation factors between valve trace elements (Mg/Ca or Sr/Ca ratios as well as D_{Mg} or D_{Sr}) and environmental parameters (Temperature and water Mg/Ca or Sr/Ca ratios) as well as valve stable isotope compositions ($\delta^{13}C$ and $\delta^{18}O$) were determined for adults. These results are presented in Table 5.2, 5.5, and 5.7 for Candoninae and Cyprididae, and Cytheroidea, respectively. Respective plots are presented in electronic appendixes EA-2, EA-4, and EA-6.

3. Discussion

To evaluate the relation between environmental conditions and ostracod trace element contents, it is possible, thanks to the isotopic analyses, to examine the geochemical results without considering environmental parameters. As $\delta^{18}O$ values of water vary only insignificantly in comparison to temperature during the studied years, $\delta^{18}O$ values of ostracods can be used in our dataset as proxy of water temperature during valve calcification. In addition, fractionation of oxygen isotopes is identical within each subfamily and quite comparable within families. Hence, variations of $\delta^{18}O$ values among different species belonging to the same family can be interpreted as a change in water temperature. On the other hand, carbon isotopes of ostracod valves are, except for some rare species, in equilibrium with water DIC. For burrowing ostracods (infaunal forms), carbon isotopic compositions of the valves reflect sediment pore water conditions. On the other hand, $\delta^{13}C$ values of ostracods living in open water of the littoral zones (epifaunal forms) reflect the photosynthetic activity. As photosynthetic activity controls calcite precipitation, $\delta^{13}C$ values of epifaunal species can be used as a proxy for water Mg/Ca and Sr/Ca ratios. Hence, Mg/Ca and Sr/Ca ratios of ostracod valves can be easily compared indirectly to water temperature, microenvironments and water Mg/Ca and Sr/Ca ratios via carbon and oxygen isotope compositions measured on the same samples.

3.1. Geochemistry of Candonidae Valves

In Figure 5.4, the different species can be regrouped according the type of relations that can be observed: first group includes *Candona candida*, *Candona neglecta*, and *Fabaeformiscandona caudata* (1); second one *Pseudocandona compressa* (2); and third one *Cypria ophtalmica* (3).

1) Results for the first group present no clear relationships except for a slight correlation between Sr/Ca ratios and $\delta^{13}C$ values (Fig. 5.4 C) and an almost insignificant negative relationship between Sr/Ca ratios and $\delta^{18}O$ values (Fig. 5.4 D).

For $\delta^{13}C$ values lower than –7 ‰, Sr/Ca ratios present a large variability and no visible trend. The relation between $\delta^{13}C$ values and Sr/Ca ratios is apparently higher when $\delta^{13}C$ values are higher than –7 ‰. $\delta^{13}C$ values lower than –6 to –7 ‰ are typical for specimens that moult in sediment interstitial pores where remineralisation of sedimentary organic matter releases a high amount of light carbon. Values higher that –6 to –7 ‰ reflect, in contrast, conditions in open water. There, a significant enrichment in ^{13}C occurs during warm season due to the photosynthetic activity.

On Figure 5.4 A and C, Mg/Ca and Sr/Ca ratios for 'pore water' and $\delta^{13}C$ values are not correlated. This suggests that Sr/Ca and Mg/Ca ratios of infaunal species reflect the high chemical variability of sediment pore water. These specimens can therefore in any way not be used for reconstruction of past conditions in open water.

For 'open water' $\delta^{13}C$ values, the correlation between Sr/Ca and $\delta^{13}C$ values (Fig. 5.4 C) is better than that between Sr/Ca and $\delta^{18}O$ values (Fig. 5.4 D). This suggests that Sr/Ca of ostracod valves are principally controlled by water Sr/Ca ratios and the microenvironment rather than by water temperature. This assumption is supported by the results of Engstrom and Nelson (1991), who reported no temperature dependency for strontium uptake in *Candona Rawsoni*. The slight correlation observed in Figure 5.4 D can thus be explained by the simple fact

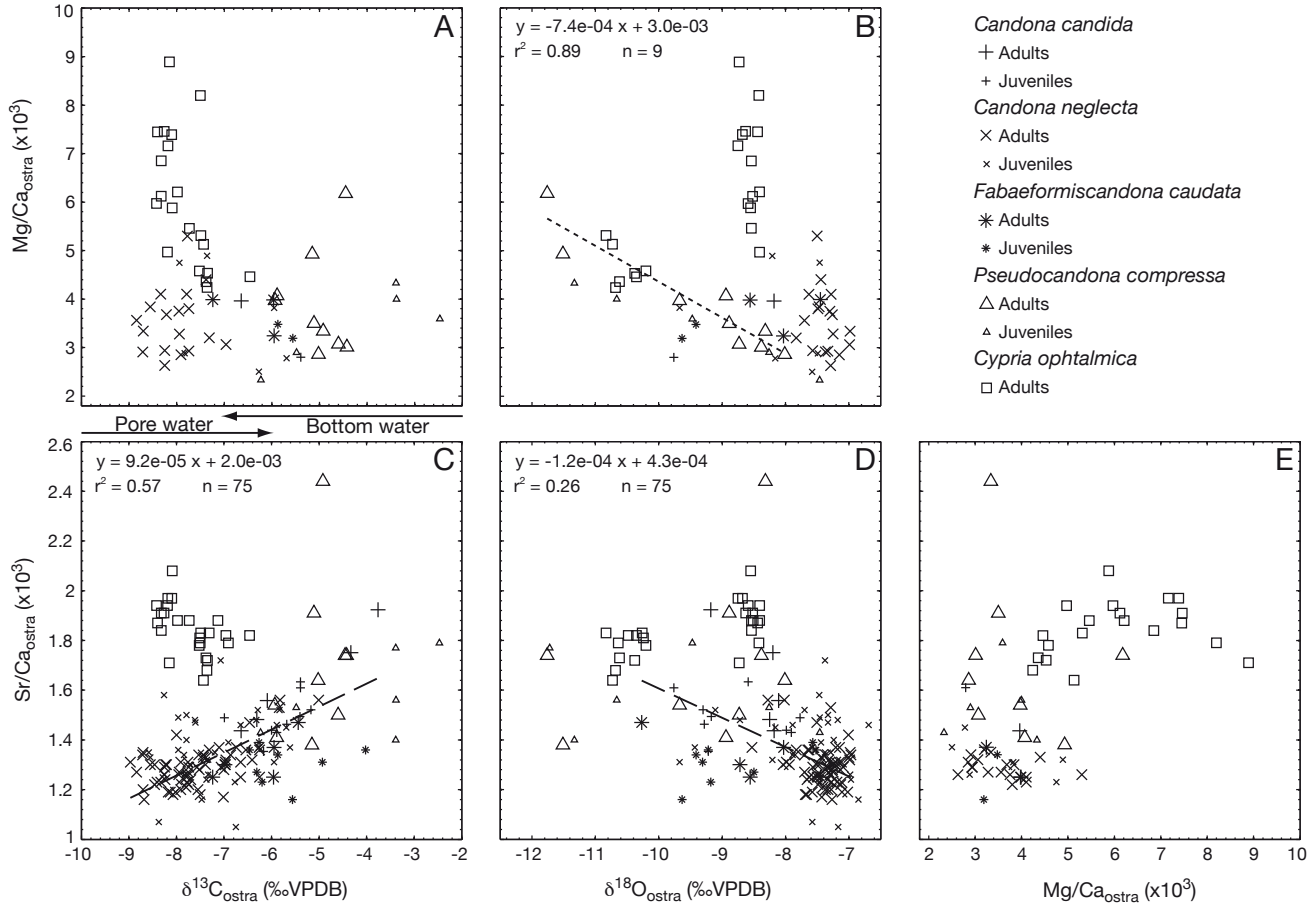


FIGURE 5.4
Mg/Ca and Sr/Ca ratios against $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Candonidae. Dashed lines represent linear regressions calculated for groupe 1 (*C. candida*, *C. neglecta* and *F. caudata*; see text); dotted line represents linear regression calculated for *P. compressa*.

that the period of high water Sr/Ca ratios corresponds to the warmer period. It may yet also be explained by a slight temperature dependency of strontium uptake during valve calcification (see below).

2) *Pseudocandona compressa* (group n°2) presents a totally different behaviour regarding trace element partitioning; and this even if this species is taxonomically related to the species of the first group. Mg/Ca ratios for this species present a strong negative relationship with $\delta^{18}O$ values (Fig. 5.4 B). However, no relations are observed in the other plots. The fact that Mg/Ca ratios correlate with $\delta^{18}O$ values but not with $\delta^{13}C$ values suggests that water temperature controls magnesium incorporation in *Pseudocandona compressa*. The different trace element partitioning observed between this species and the one of the first group may be related to differences in biomineralisation processes. Another possibility is that habitat plays an important role in trace element content of ostracod valves. *Pseudocandona compressa* is typically a littoral species and is only found at 2 and 5 m water depths whereas all the other Candonidae species occur only from 13 to 70 m water depths in Lake Geneva. Water in littoral zones experiences large seasonal temperature and chemical variations. Variations are, in contrast, weak to nonexistent in deeper sites. De Deckker and co-authors (1999) suggested that for *Cyprideis*, temperature dependency for magnesium uptake increases with increasing water Mg/Ca. In addition, the authors suggested that temperature dependency of magnesium uptake is low at low temperatures but strong at high temperature. Strontium uptake has, in contrast, the opposite behaviour, i.e. a slight temperature dependency at low temperature but no temperature dependence at higher temperatures. In sublittoral and deep zones, temperature remains relatively low throughout the year whereas water temperatures in the littoral zone reach high values during summer. In addition, Mg/Ca ratios attain much higher values in the littoral zone than in deeper zones, favouring a stronger dependence

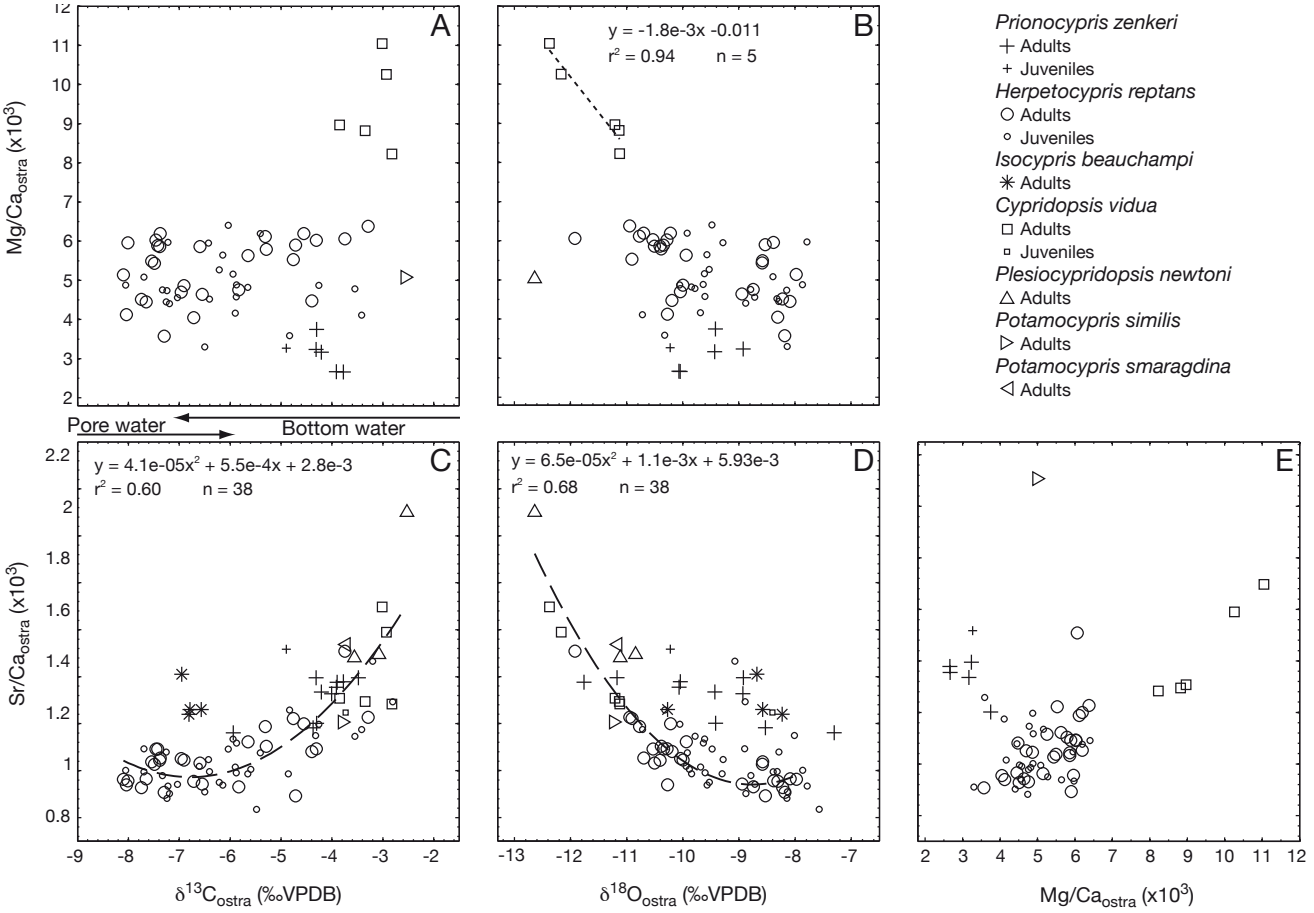


FIGURE 5.5
Mg/Ca and Sr/Ca ratios against $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Cyprididae. Dashed lines represent linear regressions calculated for Cyprididae except *P. zenkeri* and *I. beauchampi*; dotted line represents linear regression for *C. vidua*.

of magnesium uptake. Therefore, the effect of temperature and composition of water on magnesium and strontium uptake postulated by De Deckker and co-authors (1991) may explain our observations.

3) *Cypria ophtalmica* (third group) is taxonomically distinct from Candoninae as it belongs to the Cyclocypridinae Subfamily. Values for this species have absolutely no correlation between the different parameters. It should be noted that this species has an oxygen isotope vital effect that is approximately 1 ‰ lower than the vital effect determined for Candoninae species. In addition, the carbon isotope composition is not at equilibrium but depleted by one or more per mil (*Chapter V-1*). Hence, care should be taken when comparing this species to the others. The very high variability and non-coherence obtained for Mg/Ca and Sr/Ca ratios as well as relatively high Mg/Ca and Sr/Ca ratios found for this species might be linked to the specific structure of the valves. Keyser and Walter (2004) observed that the calcified cuticle of this species consists mostly of amorphous calcium carbonate that has not recrystallised to calcite crystallites during final stages of valve calcification. Several studies observed that magnesium content of non-completely calcified valves was abnormally high (Chivas et al., 1983, 1986, Palacios-Fest and Dettman, 2001). Non-coherent and relatively high magnesium and strontium content in *Cypria ophtalmica* valves may, therefore, be explained by the fact that the valves do not recrystallise in the final calcification stage as in other Candonidae but consist mostly of amorphous calcium carbonate as all ostracod valves do during initial valve calcification stage.

For all Candonidae species, no relationship exists between magnesium and strontium content in the valves. If this is correct over larger a range of values, it implies that, for Candonidae, uptake mechanisms are different for the two cations.

3.2. Geochemistry of Cyprididae Valves

Figure 5.5 illustrates that for Cyprididae species, except *Prionocypris zenkeri* and *Isocypris beauchampi*, the same patterns for magnesium and strontium uptake are presented.

In general, Mg/Ca ratios have no clear relationships with the isotopic compositions of the valve (Fig. 5.5 A and B). An interesting point is that for $\delta^{13}C$ values indicating a pore water influence, the Mg/Ca ratios for *Herpetocypris reptans* present a high variability (Fig. 5.5 A). This can be either due to the high variability of condition/chemistry found in pore water or simply to the higher variability of Mg/Ca ratios found in pore waters. In Figure 5.5 B, Mg/Ca ratios tend to decrease with increasing $\delta^{18}O$ values. This relationship may actually be blurred by the influence of pore water chemistry and might be higher in exclusive open water conditions.

Sr/Ca ratios present, in contrast, a good relationship of the second order with $\delta^{13}C$ values (Fig. 5.5 C) as well as with $\delta^{18}O$ values (Fig. 5.5 D). For carbon isotopes, the Sr/Ca ratios remain relatively constant for 'pore water' conditions, but increase with $\delta^{13}C$ values for 'open water' conditions (Fig. 5.5 D). For ostracods, moulting in interstitial sediment pores, ostracod $\delta^{13}C$ values are dictated by the decrease of $\delta^{13}C_{DIC}$ values found along sediment depth profiles. On the other hand, $\delta^{13}C$ values of ostracods living in 'open water' reflect photosynthetic activity, which may vary itself concomitantly with temperature. The strong relationship observed between 'open water' $\delta^{13}C$ values and Sr/Ca ratios suggest, therefore, that the water Sr/Ca ratios control ostracod valve strontium contents. However, in Figure 5.5 C, the relationship between $\delta^{18}O$ values and Sr/Ca ratios can be followed over the whole range of $\delta^{18}C$ values. This observation suggests that it is actually the water temperature that controls strontium uptake in Cyprididae ostracod valves. However, it is once again not possible to distinguish the effect of a change in water Sr/Ca ratios from that of temperature.

When Mg/Ca ratios are plotted against Sr/Ca ratios, both ratios increase concomitantly (Fig. 5.5 E). Hence, the same factor must control magnesium and strontium uptake. If this is temperature and/or water trace element content then, ostracod Mg/Ca ratios should present a better correlation with $\delta^{13}C$ and/or $\delta^{18}O$ values. The weaker relations found for Mg/Ca ratios (Fig. 5.5 A and B) in comparison to Sr/Ca ratios (Fig. 5.5 C and D) might be due to a stronger effect of pore water chemistry on Mg/Ca ratios than Sr/Ca ratios. Besides, during the analyses, magnesium content was much more affected by contamination and more difficult to measure. Thus, it is possible that higher analytic uncertainties are the cause of the lower relationship found for Mg/Ca ratios. Linear positive relationships between Mg/Ca and Sr/Ca ratios was also observed for the *Herpetocypris intermedia* specimens collected in a Mediterranean spring (Wansard and Mezquita, 2001). These results, together with the present dataset suggest that covariance of magnesium and strontium is standard in Cyprididae.

The two other species, *Prionocypris zenkeri* and *Isocypris beauchampi*, present no clear relationships. In addition, values for both species plot differently in the diagrams compared to other Cyprididae species. The first species, *P. zenkeri*, is described as a species living exclusively in flowing water. Its presence in lakes is generally attributed to passive rafting from nearby streams. However, $\delta^{18}O$ values measured on specimens collected in Lake Geneva suggest that the valves crystallised in lake water (*Chapter V-1*, *Appendix I*). Thus, it is not clear whether another mechanism controls trace element uptake for this species or if the specimens did not actually form in lake water. The second species, *I. beauchampi*, inhabits the deeper zones of Lake Geneva compared to other Cyprididae. This species was found at 13 and 33 m water depth. It is possible that at these depths, pore water has a higher effect on ostracod valve trace element contents. This may explain the relative enrichment in strontium of the valves. On the other hand, this species has very thin valves. A different structure of the carapace and/or lower calcification might also account for the difference observed for this species relative to the other Cyprididae.

3.3. Geochemistry of Cytheroidea Valves

In Figure 4, the three species belonging to the Superfamily Cytheroidea each present different trace element contents. *Limnocythere inopinata* and *Limnocytherina sanctipatricii* are taxonomically closely related as both belong to the Limnocytherinae subfamily. Both species have equivalent oxygen isotope vital effects. In addition, carbon isotope compositions of both species are depleted in ^{13}C relative to values of calcite in equilibrium with DIC. When corrected for vital effect, $\delta^{13}C_{ostra}$ values represent 'open water' conditions rather than a 'pore water' influence. The two species show an increase of Sr/Ca ratios with increasing $\delta^{13}C$ values and a decrease of Sr/Ca ratios with increasing $\delta^{18}O$ values

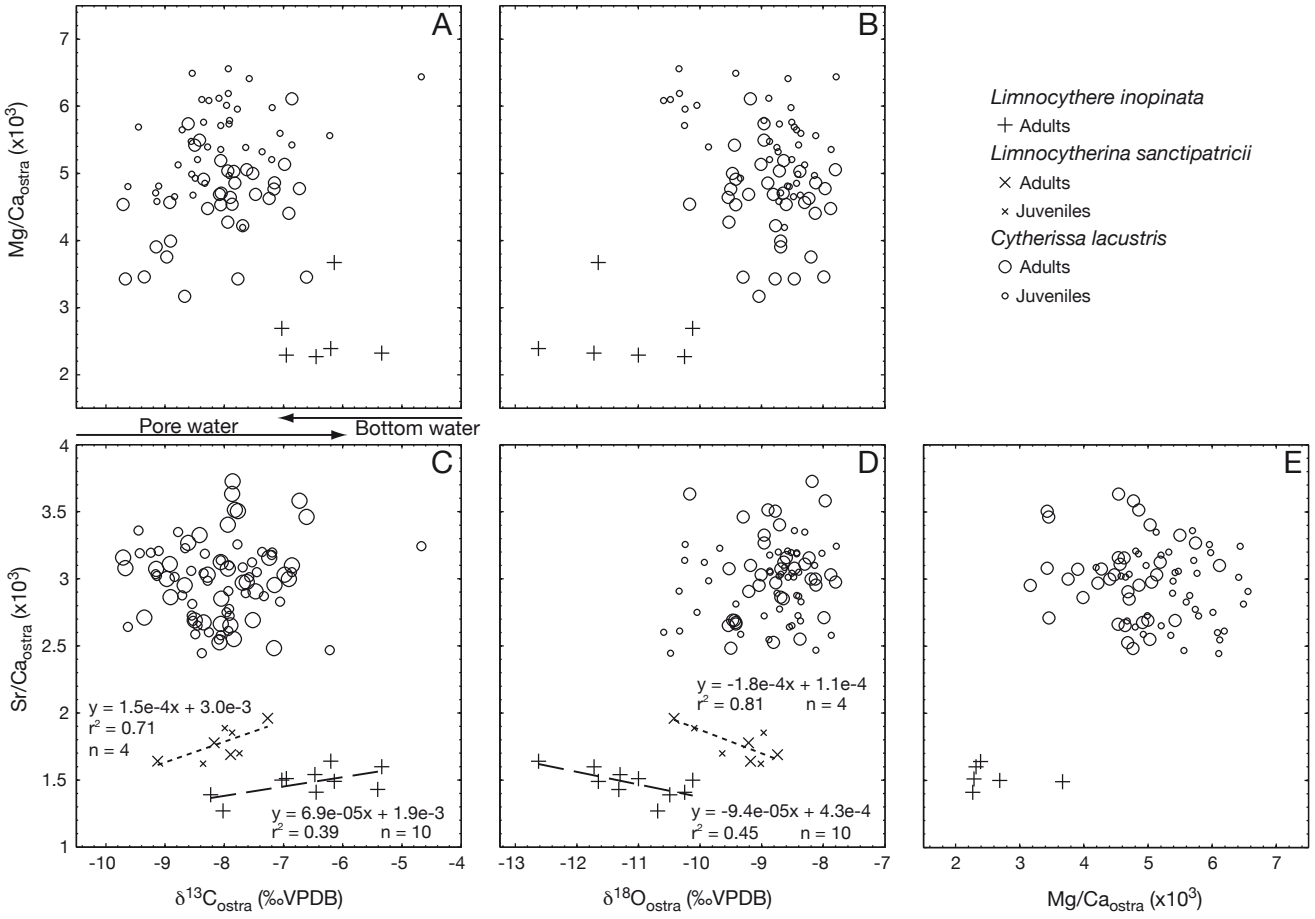


FIGURE 5.6
Mg/Ca and Sr/Ca ratios against $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Cytheroidea. Dashed lines represent linear regressions calculated for *L. inopinata*; dotted lines represent lineat regressions for *L. sanctipatricii*.

(Fig. 4D), suggesting that strontium contents of both species reflects water temperature and/or variations of Sr/Ca ratio of water. The correlation lines for both species present a significant offset among them but both series of points are in the main parallel.

In contrast, values for *Cytherissa lacustris* present absolutely no correlations. All $\delta^{13}C$ values correspond to pore water conditions. In addition, both Sr/Ca and Mg/Ca ratios are high and present values that are very variable. These observations may be attributed to the higher chemical variability observed in sediment pore water or to a specific mechanism for trace element uptake.

3.4. Trace Element Partitioning vs. Environmental Factors

To further examine the factors controlling trace element uptake during valve calcification, the Mg/Ca and Sr/Ca ratios as well as D_{Mg} and D_{Sr} can be plotted against environmental factors, such as temperature, and Mg/Ca or Sr/Ca ratios of water. Correlation factors between ostracod Sr/Ca and Mg/Ca ratios and temperature, Sr/Ca and Mg/Ca ratios of water, and ostracod $\delta^{18}O$ and $\delta^{13}C$ values are presented in Tables 5.3, 5.5, and 5.7 for Candonidae, Cyprididae, and Cytheroidea, respectively. Correlation factors where also determined for D_{Sr} and D_{Mg}. The respective plots and linear regression lines are given in electronic appendixes EA-2, EA-4, and EA-6.

A general inspection of Tables 5.3, 5.5, and 5.7 and electronic annexes EA-2, EA-4, and EA-6 reveals that

trace element partitioning are very variable. However, some important points emerge:

1) In general, D_{Mg} or D_{Sr} increase with temperature for the case where ostracod Mg/Ca or Sr/Ca ratios increase with temperature.

2) D_{Mg} and D_{Sr}, in contrast, tend to decrease with increasing Mg/Ca or Sr/Ca ratios of water.

3) For Cyprididae, magnesium and strontium uptake is similar, whereas uptake of both cations seem to be independent in Candonidae and Cytheroidea.

Given the large number of results to examine and the high variability of magnesium and strontium concentrations, a synthetic approach was adopted to help understand the different types of relationships observed and to discuss the factors that control the magnesium and strontium partitioning. Because of the complexity of the environment and the number of variables, neither quantitative nor thermodynamic models were applied. The approach used here focuses principally on the type of correlations observed between the different factors. To classify and explain the different correlations observed within the dataset, the consequences of different types of controls on ostracod trace element content and partitioning coefficients were examined in theory. Five types of controls were examined, which are schematically illustrated in Figure 5.7.

The hypotheses for the models are based on variations of environmental parameters and ostracod geochemistry observed in Lake Geneva. As such the temperature, X/Ca ratios of water (X designing either Mg or Sr), and $\delta^{13}C_{DIC}$ values vary concomitantly in the model (*Chapter IV*). Ostracod $\delta^{18}O$ values decrease linearly with temperature and ostracod $\delta^{13}C$ values can be used as a proxy for water X/Ca ratios. Different types of control on ostracod trace element partitioning were added to form five types of trace element partitioning behaviour:

– Model Type A considers that the partition coefficient is constant.

– Model Type B considers that X/Ca ratios of ostracod are directly dependent on temperature without any dependence to X/Ca ratios water. As the X/Ca ratios of water and temperature vary concomitantly, a positive relationship between the X/Ca ratios of ostracod and the X/Ca ratios of water is found although the X/Ca ratios of water have no influence on the X/Ca ratios of ostracod.

TABLE 5.2
Mean partition coefficients for Mg and Sr determined for the Candonidae. See electronic annexe EA-1 for respective histograms.

Species	n=	D_{Mg}	std	n=	D_{Sr}	std
Candona candida	1	0.0183	-	4	0.354[t]	0.070
Candona neglecta	13	0.0165	0.0031	36	0.296	0.040
Fabaeformiscandona caudata	3	0.0177	0.0022	5	0.297	0.035
Pseudocandona compressa	9	0.0159[t]	0.0033	9	0.343	0.066
Cypria ophtalmica	15	0.0302	0.0064	20	0.464	0.065

TABLE 5.3
Correlation coefficients for Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr} vs. water temperature, respective Mg/Ca and Sr/Ca ratios of water as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Candonidae. Values in bold represent high correlation factors and/or particularly interesting relationships. See electronic annexe EA-2 for respective plots and linear regression lines.

Species		Mg/Ca r =	D_{Mg} r =	Sr/Ca r =	D_{Sr} r =
Candona candida	T (°)	-	-	**0.93**	**0.98**
	X/Ca_{H2O}	-	-	-0.73	**-0.90**
	$\delta^{13}C_{ostra}$	-	-	**0.98**	0.90
	$\delta^{18}O_{ostra}$	-	-	**-0.81**	-0.95
Candona neglecta	T (°)	0.12	0.18	0.34	-0.40
	Sr/Ca_{H2O}	0.14	0.03	-0.03	**-0.90**
	$\delta^{13}C_{ostra}$	0.12	0.17	**0.58**	-0.17
	$\delta^{18}O_{ostra}$	-0.27	-0.32	-0.31	0.29
Fabaeformiscandona caudata	T (°)	-	-	**0.74**	**0.73**
	X/Ca_{H2O}	-	-	-0.01	**-0.79**
	$\delta^{13}C_{ostra}$	-	-	**0.71**	0.84
	$\delta^{18}O_{ostra}$	-	-	**-0.76**	-0.78
Pseudocandona compressa	T (°)	**0.95**	**0.91**	-0.38	-0.69
	X/Ca_{H2O}	0.77	0.56	0.17	**-0.36**
	$\delta^{13}C_{ostra}$	0.01	-0.18	**0.32**	0.07
	$\delta^{18}O_{ostra}$	**-0.94**	-0.88	0.34	0.70
Cypria ophtalmica	T (°)	-0.60	-0.67	-0.61	-0.69
	X/Ca_{H2O}	-0.54	-0.62	-0.55	**-0.40**
	$\delta^{13}C_{ostra}$	-0.36	-0.42	-0.50	-0.60
	$\delta^{18}O_{ostra}$	0.51	0.58	0.63	0.75

TABLE 5.4
Mean partition coefficients for Mg and Sr determined for the Cyprididae. See electronic annexe EA-3 for respective histograms.

Species	n=	D_{Mg}	std	n=	D_{Sr}	std
Prionocypris zenkeri	5	0.0134	0.0020	8	0.274	0.015
Herpetocypris reptans	22	0.0242	0.0035	22	0.227	0.029
Isocypris beauchampi	-	-	-	4	0.273	0.019
Cypridopsis vidua	5	0.0386	0.0018	5	0.267 [t]	0.022
Plesiocypridopsis newtoni	-	-	-	1	0.236	-
Potamocypris	1	0.0011	-	4	0.317 [t]	0.032

– Model Type B' is a sub-model of model Type B. In this case, initial hypothesis that water X/Ca ratios vary concomitantly with temperature is substituted by the hypothesis that water X/Ca ratios are constant. The other initial hypotheses are preserved.

– Model Type C considers that ostracod D_X is temperature dependent. In this case, the effect of the increase of the X/Ca ratio of water with temperature is added to the effect of preferential uptake of element X with increasing water temperature.

– Model Type D considers that ostracod X/Ca ratios are constant, i.e. the ostracods fix the amount of trace element contained in its carapace independently of the external conditions.

– Model Type E assumes that the amount of element X cannot exceed a certain amount in the valve. In other words, the amount of element X increases until saturation. This type of relation can be estimated using a logarithmic function.

Strontium and magnesium incorporation of species analysed in Lake Geneva as well as in previous studies can be compared to the different model types. The types describing the best the relations observed for the ostracod species are summarized in Table 5.8. For some species, several model Types are described. This is due to the fact that, in a single species, one of the correlations observed can be typical for one type of model, whereas another correlation can be typical for another type of model. Thus, the model types are given in sequence according to their similarity with the measured data, the first one being the most similar and the similarity according to correlation factor (r) decreasing from left to right within the column of the Table 5.8. The establishment of these theoretical models and comparison with measured values reveals interesting points:

1) Type A and Type B can, as already stated above, be very difficult to discriminate. It could be expected that for Type A, the correlation is higher between ostracod X/Ca ratios and those of water relative to the ostracod X/Ca ratios and water temperature. In contrast, the opposite must be observed for Type B, i.e. higher correlation between ostracod X/Ca ratios and water temperature than between ostracod X/Ca ratios and those of water. This approach was used by Dettman and co-authors (2002) to demonstrate that temperature controlled the magnesium and strontium uptake in *Herpetocypris intermedia*.

However, a higher correlation coefficient may not necessarily imply the given model is correct. In the

TABLE 5.5
Correlation coefficients for Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr} ratios vs. water temperature, respective Mg/Ca and Sr/Ca ratios of water, as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Cyprididae. Values in bold represent high correlation factors and/or particularly interesting relstionships. See electronic annexe EA-2 for respective plots and linear regression lines.

Species		Mg/Ca r =	D_{Mg} r =	Sr/Ca r =	D_{Sr} r =
Prionocypris zenkeri	T (°)	-0.61	-0.73	**0.75**	0.59
	X/Ca_{H2O}	0.00	-0.18	**0.81**	0.58
	$\delta^{13}C_{ostra}$	-0.88	-0.92	**0.65**	0.29
	$\delta^{18}O_{ostra}$	0.71	0.81	**-0.71**	-0.49
Herpetocypris reptans	T (°)	0.76	0.37	**0.90**	**0.79**
	Sr/Ca_{H2O}	0.47	-0.09	0.53	-0.16
	$\delta^{13}C_{ostra}$	0.23	0.18	**0.57**	0.01
	$\delta^{18}O_{ostra}$	-0.57	-0.23	**-0.84**	-0.78
Isocypris beauchampi	T (°)	-	-	-0.31	0.74
	X/Ca_{H2O}	-	-	0.49	-0.66
	$\delta^{13}C_{ostra}$	-	-	-0.68	0.44
	$\delta^{18}O_{ostra}$	-	-	0.12	-0.86
Cypridopsis vidua	T (°)	**0.96**	0.25	**1.00**	**0.95**
	X/Ca_{H2O}	**0.93**	0.16	**0.98**	**0.91**
	$\delta^{13}C_{ostra}$	0.24	-0.68	**0.42**	0.73
	$\delta^{18}O_{ostra}$	**-0.97**	-0.31	**-1.00**	-0.92
Potamocypris	T (°)	-	-	**0.98**	**0.98**
	X/Ca_{H2O}	-	-	**0.99**	**0.97**
	$\delta^{13}C_{ostra}$	-	-	**0.84**	0.84
	$\delta^{18}O_{ostra}$	-	-	**-0.99**	-0.99

TABLE 5.6
Mean partition coefficients for Mg and Sr determined for the Cytheroidea species. See electronic annexe EA-5 for respective histograms.

Species	n=	D_{Mg}	std	n=	D_{Sr}	std
Limnocythere inopinata	6	0.0065	0.0003	10	0.306	0.023
Limnocytherina sanctipatricii	-	-	-	6	0.390[t]	0.035
Cytherissa lacustris	28	0.0202	0.0029	29	0.740	0.109

TABLE 5.7
Correlation coefficients for Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr} ratios vs. water temperature, respective Mg/Ca and Sr/Ca ratios of water, as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Cytheroidea. Values in bold represent high correlation factors and/or particularly interesting relstionships. See electronic annexe EA-6 for respective plots and linear regression lines.

Species		Mg/Ca r =	D_{Mg} r =	Sr/Ca r =	D_{Sr} r =
Limnocythere inopinata	T (°)	0.04	-0.53	**0.57**	-0.21
	X/Ca_{H2O}	-0.11	-0.63	0.51	-0.51
	$\delta^{13}C_{ostra}$	0.04	0.15	**0.62**	0.04
	$\delta^{18}O_{ostra}$	-0.12	0.43	**-0.67**	0.15
Limnocytherina sanctipatricii	T (°)	-	-	**0.75**	**0.92**
	Sr/Ca_{H2O}	-	-	0.03	-0.60
	$\delta^{13}C_{ostra}$	-	-	**0.72**	0.76
	$\delta^{18}O_{ostra}$	-	-	**-0.62**	-0.90
Cytherissa lacustris	T (°)	0.09	0.13	-0.08	-0.95
	X/Ca_{H2O}	0.48	0.35	0.15	-0.90
	$\delta^{13}C_{ostra}$	0.47	0.45	0.15	-0.17
	$\delta^{18}O_{ostra}$	-0.13	0.22	0.13	0.45

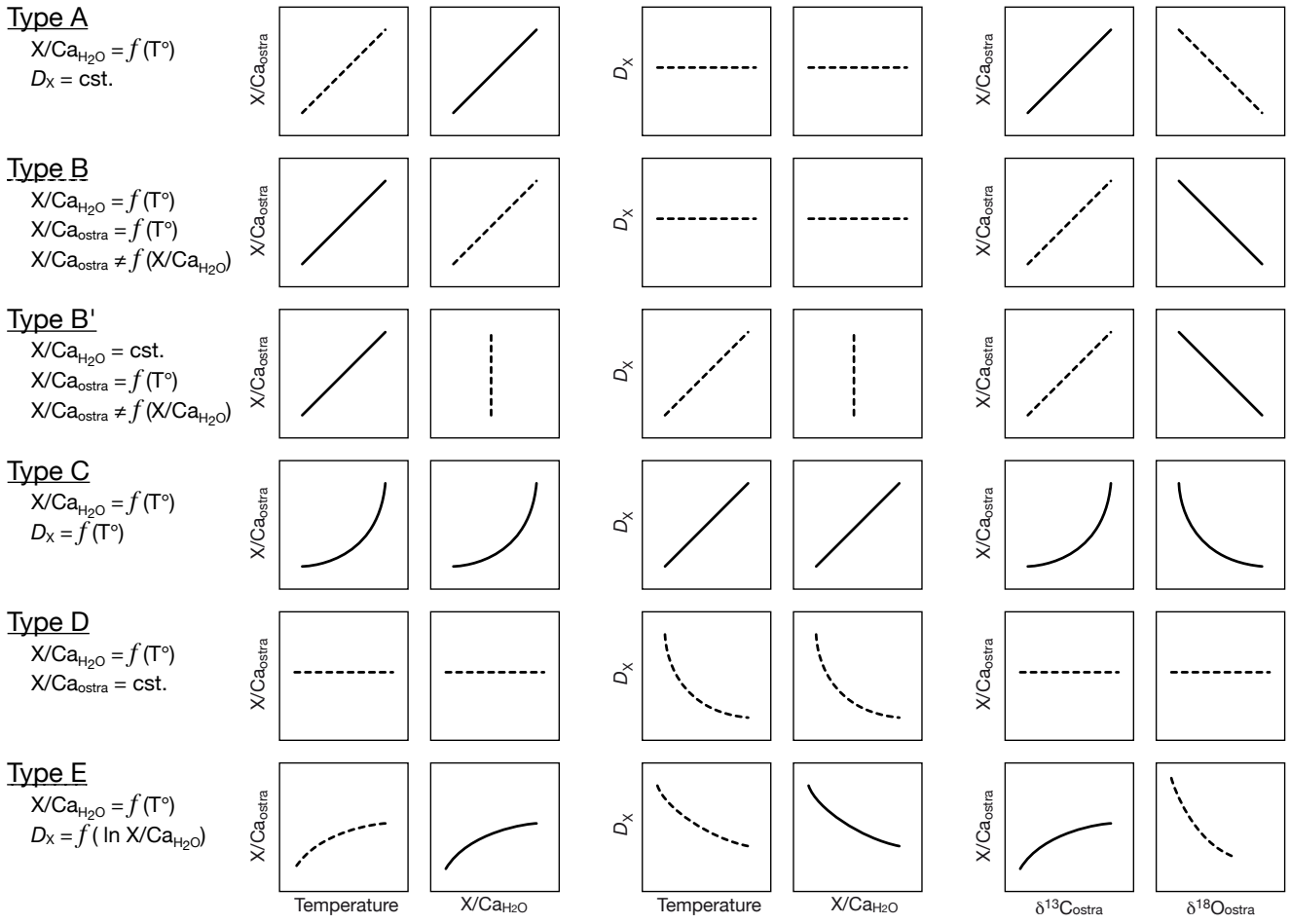


FIGURE 5.7
Theoretical relationships between ostracod X/Ca ratios (X being either Mg or Sr) and partition coefficients D_X against temperature and water X/Ca ratio as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples. The solid lines stand for higher corelation factors in comparison with the dashed lines. See text for explanation.

case of the present dataset, for example, calcification temperatures are readily estimated in contrast to the composition of the water. Three reasons explain this statement. Firstly, uncertainties are much lower for water temperature measurements than for measurements of trace element contents. Secondly, and more importantly, datasets for water temperature represent a continuous record, unlike the dataset for element ratios, which are one-point measurements. For temperature, one measurement was made each 3 hours and representative averages can be readily calculated. Only monthly measurements were made for the elemental ratios. Thirdly, in a given site, water temperature is quite homogenous whereas large variations of the chemical composition of water are expected in the different ostracod microhabitats. Hence, measured temperature of water is expected to approximate the real conditions in which the ostracod calcified its carapace better compared to the measured elemental ratios of water.

2) The only case where temperature dependency of trace element partitioning can be quantitatively described is the Type B'. The study of Palacios-Fest and Dettman (2001), for example, benefitted from these conditions. Hence, the relations determined in the present study (E.A. 2, 4, and 4) shall not be used as exclusive proxies for the trace element contents of water or as exclusive proxies for water temperature because the relations presented here might include both the variation of chemical composition of water and the effect of water temperature.

3) Type C is a kind of consensus between Type A and Type B. Results of previous studies suggest that, magnesium and strontium content in ostracod valve depends on the Mg/Ca or Sr/Ca ratios of water, but also that the incorporation of magnesium, and maybe strontium, is temperature dependent (Chivas et al., 1983, 1986; Engstrom and Nelson, 19991; De Deckker et al., 1999; Palacios-Fest and Dettman, 2001; Dettman et al., 2002; Cronin et al., 2005; Kondo et al.,

TABLE 5.8
Type of relationships between trace element contents and environmental parameters observed for the species studied in Lake Geneva and in previous studies. See Figure 5.7 for respective types of relationships.

study	species	Mg/Ca relation type	Sr/Ca relation type
Lake Geneva	**Candonidae**	(C)	none
	C. candida	-	C D
	C. neglecta	none	(D C AB)
	F. caudata	-	(D C AB)
	P. compressa	C	D
	C. ophtalmica	none	none
	Cyprididae	none	C
	P. zenkeri	-	((A))
	H. reptans	((BA DC))	C
	C. vidua	B A	C
	Potamocypris	-	C
	Cytheroidea	none	none
	L. inopinata	-	((AB))
	L. sanctipatricii	-	(B D)
	C. lacustris	none	D
Wansard & Mezquita, 2001	*Herpetocypris intermedia*	B A (C)	B A (C)
Palacios & Detmann, 2001	*Cypridopsis vidua*	B'	-
De Deckker et al., 1999	*Cyprideis australiensis*	C	C
Wansard et al., 1998	*Candona*	D	-
Kondo et al., 2005	*Xestoleberis hanaii*	C	-
Cronin et al., 2005	*Loxoconcha matagordensis*	B'	-

2005; Dwyer et al., 1995, 2002). The operation of both effects implies that X/Ca ratios increase with water temperature and the X/Ca ratios of water; accordingly a second order relationship is obtained. This is also the only type of control that leads to an increase of D_X with water temperature. Type B' can not be considered applicable here, because the hypothesis that the X/Ca ratio of water is constant is not applicable in Lake Geneva. An increase of D_x with water temperature is observed for many species in Table 5.3, 5.5, and 5.7 and in electronic appendixes EA-2, EA-4, and EA-6. Relationships of the second order are not observed when species are treated separately but Sr/Ca ratios of all Cyprididae represent a clear second order decrease with increasing $\delta^{18}O$ values. All these observations support that in many cases, trace element uptake in ostracods is comparable to model Type C. However, this model predicts an increase of D_X with increasing X/Ca ratios of water. Opposite relationships are actually observed (see following point). Hence, ostracod trace element uptake cannot be described by one simple model only.

4) A decrease of the partitioning coefficients with increasing water Mg/Ca or Sr/Ca ratios is often observed in the present dataset (point 2 above). This pattern was also observed in the dataset of a previous study (Palacios-Fest and Dettman, 2001). This relationship is also observed when a larger range of the chemical composition of water and different taxa are taken into account: the D_{Mg} decreases exponentially with increasing Mg/Ca ratios of water (Wansard et al., 1998: Holmes and Chivas, 2002). This suggests that ostracod valves can absorb a certain quantity of magnesium and/or strontium but the more the water is enriched in these elements, the less the trace elements are incorporated into the ostracods. This suggests that there is a maximum amount of magnesium and/or strontium that can be incorporated into ostracod valves. Expressed in the theoretical approach, the only way to get this relationship is if the ostracod trace element is constant (Type D) or the trace element uptake (D_X) diminishes with increasing water X/Ca ratios (Type E). From a mineralogical perspective it is known that calcite cannot take up more than a certain amount of magnesium (Mackenzie et al., 1983). However, it is unknown where the strontium and magnesium ions are located in the structure of the valves. Are they incorporated in the crystal lattice, adsorbed at the surface of the crystallite, or contained within the protein and chitin constituting the organic cuticle? It is well accepted that magnesium plays an important role

in ostracod biomineralisation processes. Magnesium content in the initial stage of valve calcification is abnormally high (Chivas et al., 1983, 1986; Palacios-Fest and Dettman, 2001). Magnesium may also act as a calcification inhibitor (Davis et al., 2000, Ziegler, 2008). Hence, a biological control must determine magnesium and strontium content of ostracod valves. Besides, it is only in a relatively short range that trace element uptake is dictated by environmental factors such as water chemistry and/or temperature. Hence, a simple mineralogical approach without taking into account biomineralisation processes is not sufficient to describe trace element uptake in ostracods (c.f. Palacios-Fest and Dettman, 2001; Dettman et al., 2002).

All things considered, no single type of model is able to explain the different relationships observed. It is possible that different effects add up during valve calcification and are revealed in a different manner within the final valve composition. However, many results remain unexplained. All this indicates how complex the incorporation of trace elements in ostracod valves is. Hence, caution is to be taken before fossil ostracod valves are used for palaeoenvironmental interpretations.

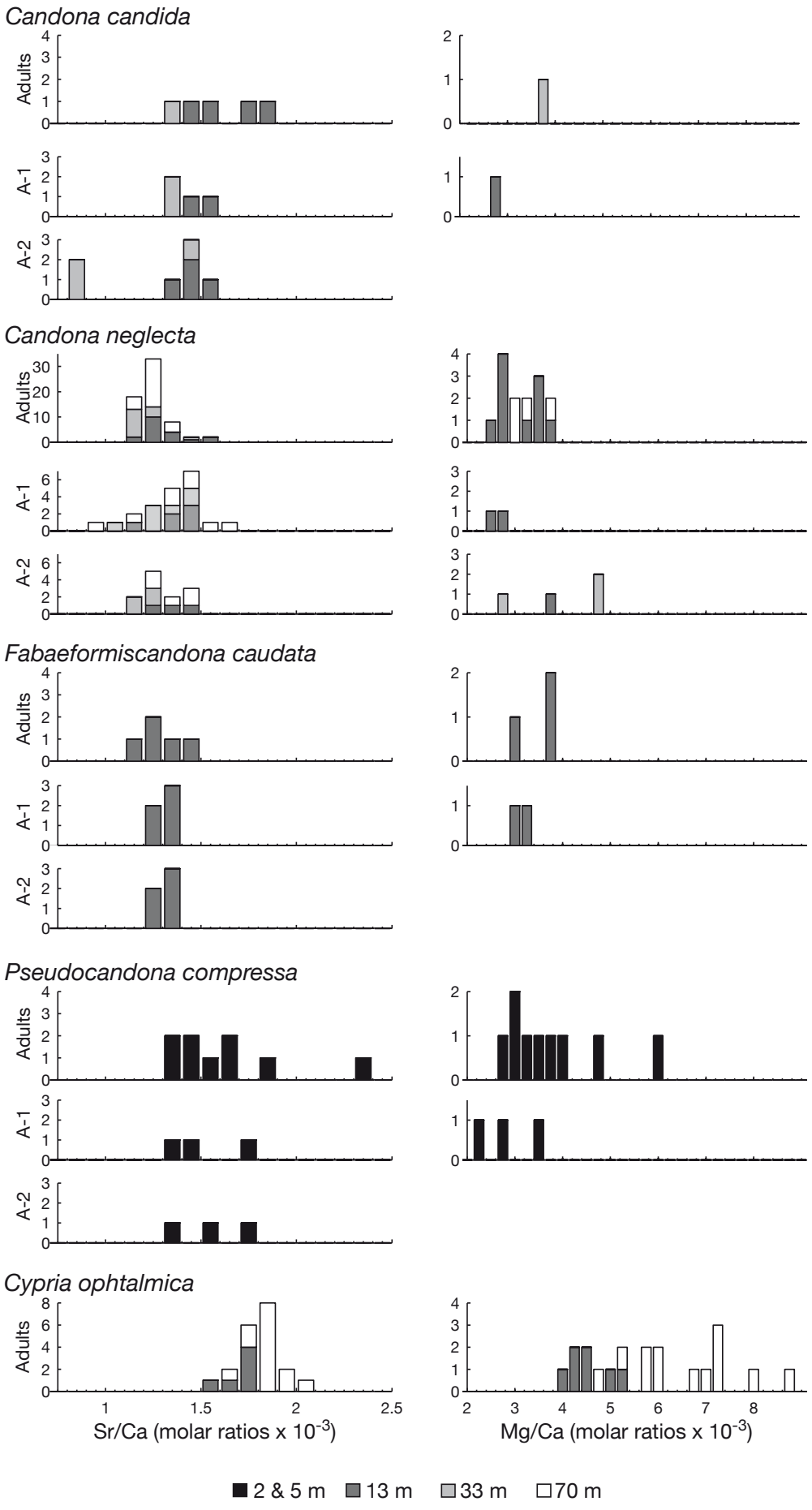
3.5. Mg/Ca and Sr/Ca ratios as Palaeoenvironmental Proxy (Conclusion)

The observations from ostracods from Lake Geneva lead to question us to whether ostracod Mg/Ca and/or Sr/Ca ratios can be used as proxies for the chemical composition of water and/or water temperature. More precisely, which situation(s) are expected to give information that actually corresponds to past conditions?

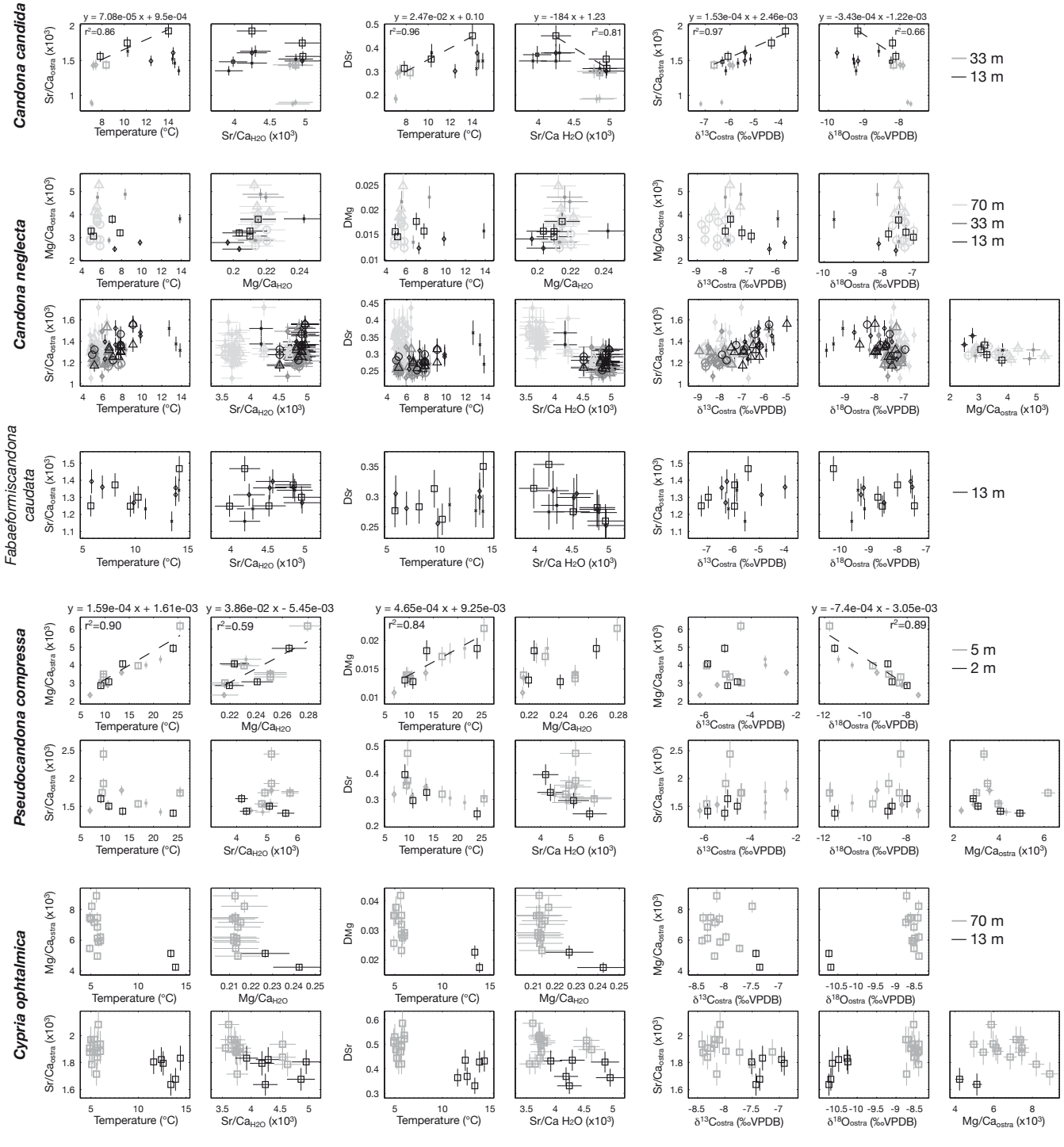
In this subsection, only systems similar to the Lake Geneva are discussed, i.e., open systems, large and deep freshwater lakes with a low amount of dissolved magnesium and strontium. As written above, De Deckker and co-authors (1999) suggested that the slope of the relation between the Mg/Ca ratio and temperature was lower at low temperature. In addition, these authors suggested that the slope of the relation between ostracod Mg/Ca ratios and temperature increases with higher Mg/Ca ratios of water. This implies that for environments with low temperatures and low Mg/Ca ratios of water, the relation expected for Mg/Ca ratios of ostracod and temperature must present a gentle slope. Hence, analytical uncertainties, and even more so the natural variability of the sample, may hide the already weak correlation of the Mg/Ca and Sr/Ca ratios of ostracods with water temperature and/or water trace element content. Besides, this low dependency implies that ostracod trace element contents are only able to register large environmental changes.

Hence, for ostracods living in the sublittoral and profundal zones, neither the Mg/Ca nor the Sr/Ca ratios of ostracod valves can be used to reconstruct past water temperature or the chemical composition of water. It is a pity because in mid latitude lakes, temperature of deep water is not always constant and can bias ostracod records and interpretations of lake water isotopic compositions. Trace element contents could theoretically permit to reconstruct past water temperature but results of the present studies clearly demonstrated that in sublittoral and profundal zones, this is not possible. The reason for this is the weak relationship between Mg/Ca or Sr/Ca ratios and water temperature in comparison to the natural variability of ostracod trace element contents. This effect is, in addition, reinforced by the effect of variability of chemistry in sediment interstitial pore water and the small change of water temperature in these environments.

It is only in the littoral zone, where effects of pore water are lower and environmental changes are larger, that valuable results from ostracod trace element contents can be obtained. However, the problem that long-term variations are lower than seasonal ones remains to be solved. As fossils used for palaeoenvironmental reconstructions reflect the average of the whole period of moulting over numerous years, a large long-term change is needed to observe variations in ostracod trace element contents. Ostracods have very strict ecological demands. Water temperature dictates their life-cycle. Besides, chemical composition of water, together with nutriment availability, and sediment texture, determine their habitat. Thus, environmental changes that are recordable by ostracod trace element contents are expected to affect the faunal assemblage as well. As a consequence, trace element analyses should be performed on species very tolerant toward environmental conditions only. A detailed or even quantitative study of ostracod faunal assemblages in parallel to geochemical analyses can then also permit a better assessment of past environmental conditions.

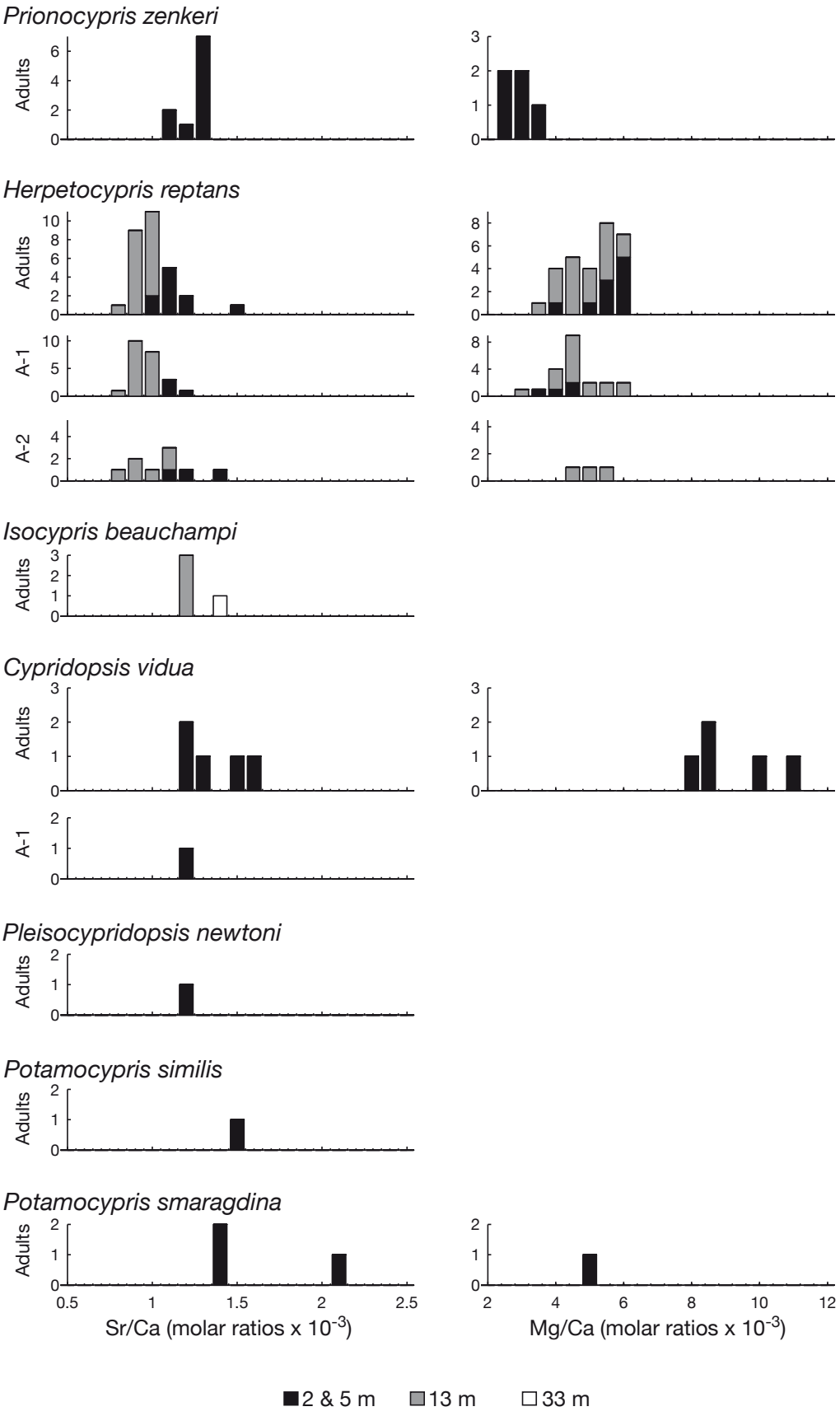


ELECTRONIC APPENDIX EA-1
Mg/Ca and Sr/Ca ratios of adult and juvenile Candonidae.

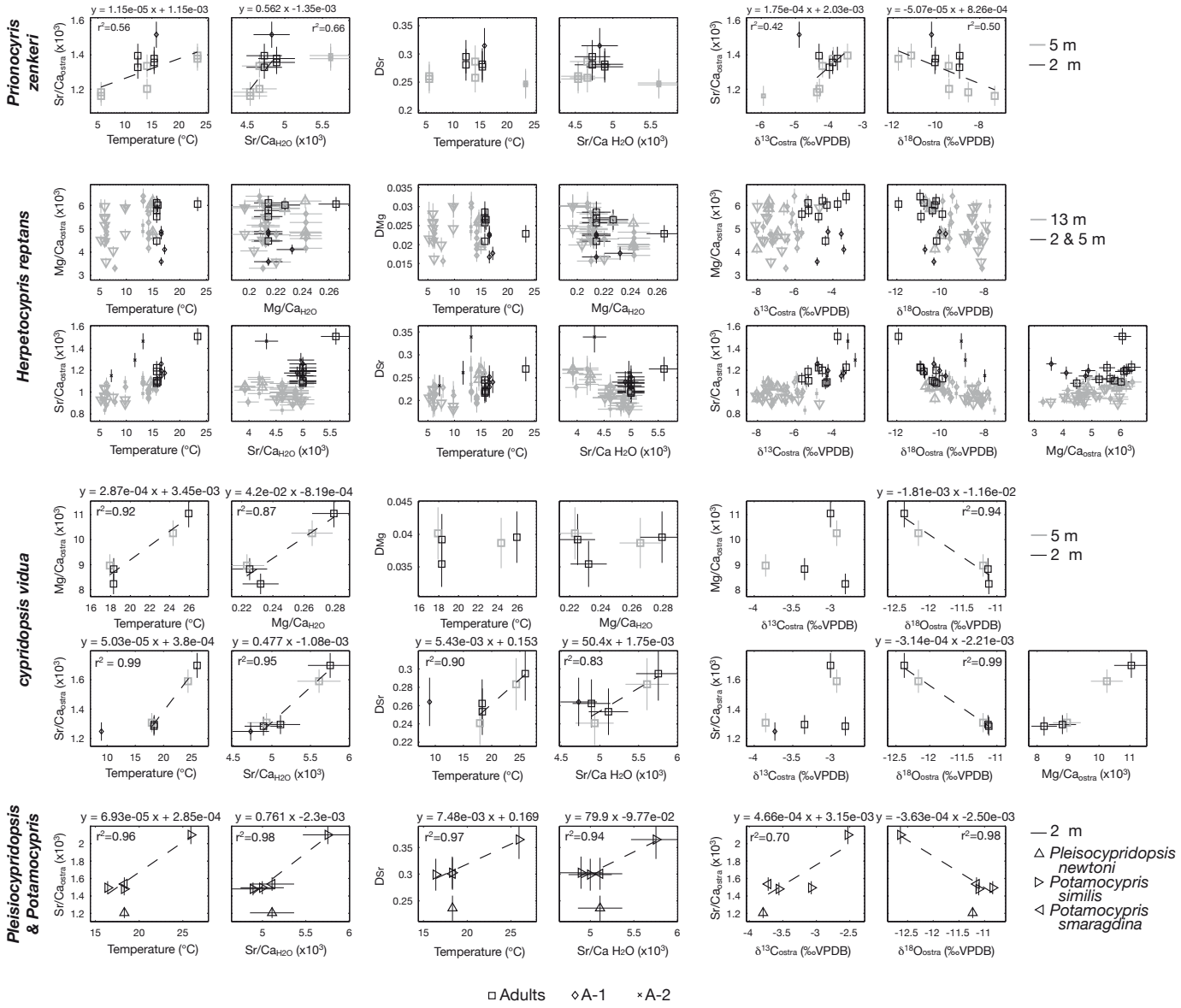


ELECTRONIC APPENDIX EA-2

Ostracod Mg/Ca and Sr/Ca ratios and respective portioning coefficient D_{Mg} and D_{Sr} plotted against temperature and respective Mg/Ca or Sr/Ca of water as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Candonidae.

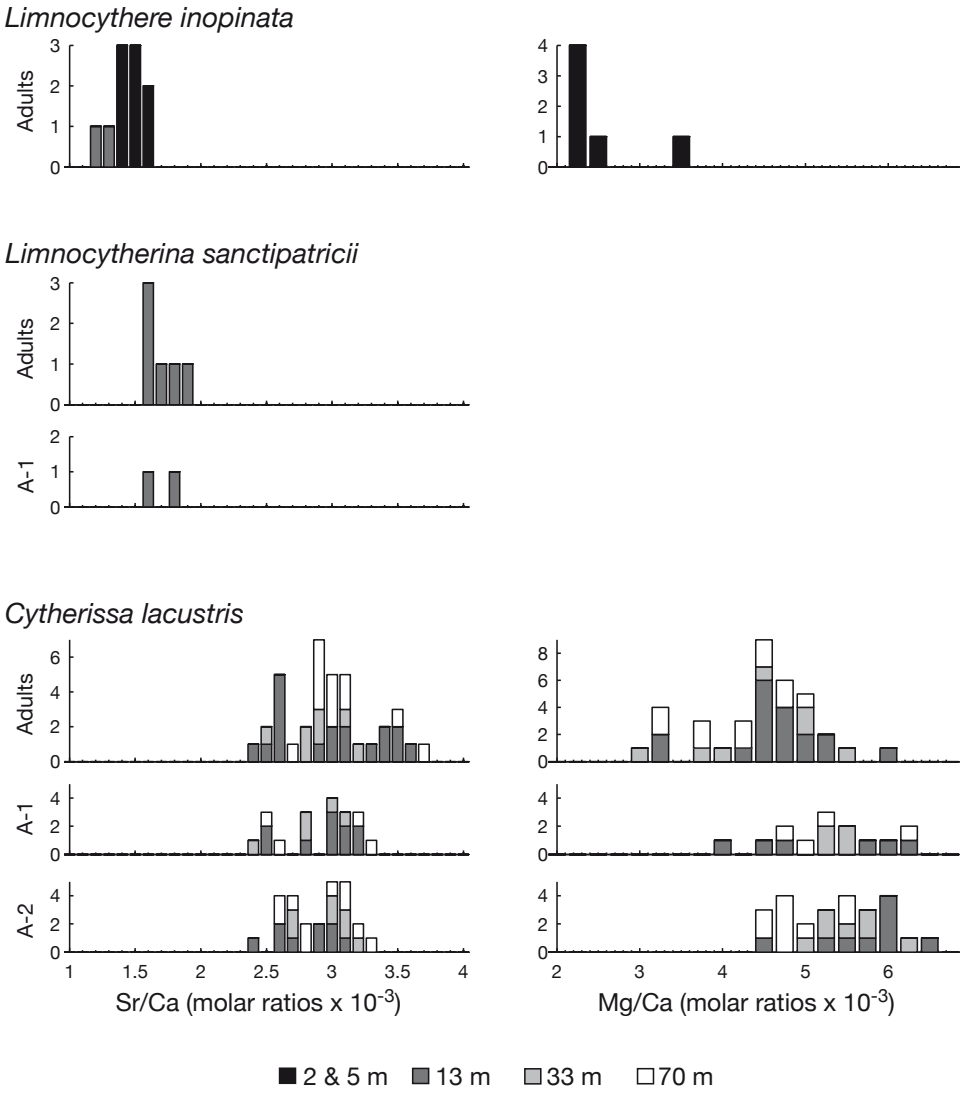


ELECTRONIC APPENDIX EA-3
Mg/Ca and Sr/Ca ratios of adult and juvenile Cyprididae.

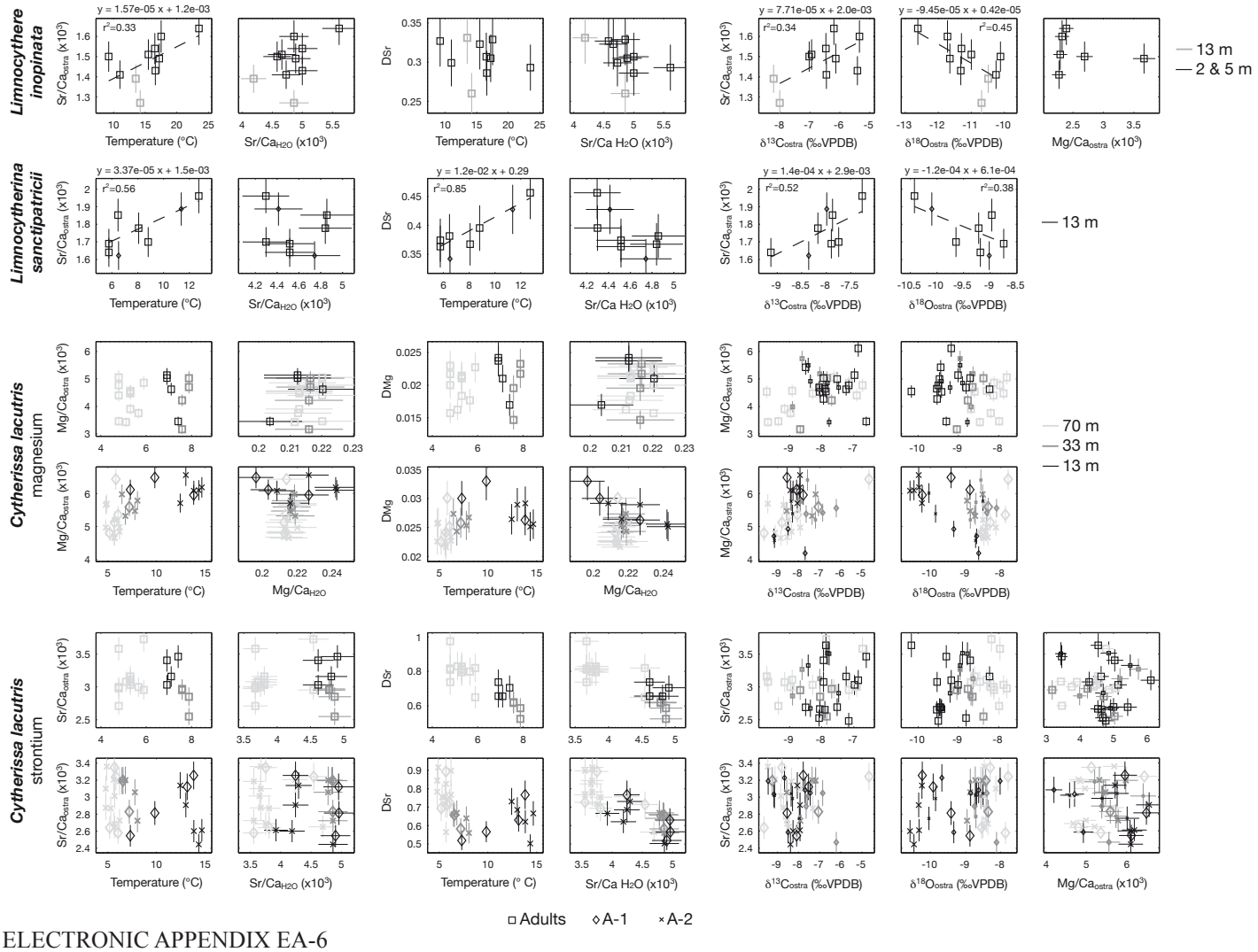


ELECTRONIC APPENDIX EA-4

Ostracod Mg/Ca and Sr/Ca ratios and respective portioning coefficient D_{Mg} and D_{Sr} plotted against temperature and respective Mg/Ca or Sr/Ca of water as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Cyprididae.



ELECTRONIC APPENDIX EA-5
Mg/Ca and Sr/Ca ratios of adult and juvenile Cytheroidea.



ELECTRONIC APPENDIX EA-6

Ostracod Mg/Ca and Sr/Ca ratios and respective portioning coefficient D_{Mg} and D_{Sr} plotted against temperature and respective Mg/Ca or Sr/Ca of water as well as $\delta^{13}C_{ostra}$ and $\delta^{18}O_{ostra}$ values measured in the same samples for Cytheroidea.

Chapter IV :

CONCLUSIONS

1. General Conclusion

The approach used for this study included a wide range of different methods. Detailed knowledge on the environmental conditions and on ostracod autoecology were related to factors controlling the ostracod shell geochemistry.

The one-year monthly sampling strategy enabled the collection of environmental data for bottom water and interstitial pore water. In littoral to sublittoral zones, carbon isotope compositions of dissolved inorganic carbon and Mg/Ca and Sr/Ca ratios of water are found to vary concomitantly with water temperature. This is due to the precipitation of calcite induced by higher photosynthetic activity as temperature and/or solar radiation intensify in summer. In deeper zones, environmental parameters remain mainly constant throughout the year. Variations of pH, DIC concentrations and carbon isotope compositions of interstitial water results from aerobic as well as anaerobic respiration, calcite dissolution and methanogenesis.

Bathymetric distribution, life-cycles, and habitats were derived for 15 ostracod species and are predominantly related to water temperature and sediment texture. A new way to present ostracod life-cycles was developed. This model, called SOWM, permits an evaluation of parameters that dictate ostracod development. It allows, in addition, a comparison of results from previous studies and gives a broader perception of ostracod autecology.

Oxygen isotope compositions of ostracod valves in Lake Geneva reflect those of water and temperature. However, up to 3 permil offsets are observed in comparison with inorganic calcite in equilibrium with water. No differences in oxygen isotopic fractionation were found among the different sampling sites, nor among juvenile, adult, male, and female specimens. In general, oxygen isotope fractionation is similar for all taxa belonging to the same subfamily. Taxa belonging to Cytheroidea have a smaller oxygen isotope fractionation hence lowest $\delta^{18}O$ values at any one temperature. Taxa belonging to Candoninae, in contrast, have the highest fractionation factors. Deprotonation of HCO_3^- and/or 'salt effect' in crystallisation sites may explain these observations.

Carbon isotope compositions of ostracod valves is not as well constrained and seems to be controlled by a complex interaction between habitat preferences and seasonal as well as spatial variations of DIC isotopic composition. For infaunal forms, carbon isotope compositions reflect mainly the variation of DIC isotopic composition in interstitial pore water. For epifaunal forms, carbon isotope compositions reflect the seasonal variation of the DIC isotopic compositions. Carbon isotope compositions of ostracod valves is in equilibrium with DIC except for *Cypria ophtalmica*, *Limnocythere inopinata*, *Limnocytherina sanctipatricii*, and maybe *Isocypris beauchampi*. These species have all in common a relatively thin shell. Non-complete valve recrystallisation during later valve calcification stages and presence of amorphous calcium carbonate may be the reason why these species are depleted in ^{13}C in comparison to equilibrium.

Trace element uptake differs significantly from species to species. For most epifaunal forms, trace element content follows the seasonal cycle, recording temperature increases and/or variations of Mg/Ca and Sr/Ca ratios of water. In contrast, epifaunal forms are predominantly related to sediment pore water chemistry.

2. Prospects

The results of this study open up promising prospects on the use of ostracod valve geochemistry as palaeoenvironmental proxies in Lake Geneva. The large dataset available for ostracod populations and detailed knowledge of species-specific autecology are of great help when ostracod fossil assemblages are studied. Fossil reworking can be assessed on the basis of the present bathymetric distributions.

Past ecological conditions may also be estimated with the help of present population densities and taxa preferential habitats. Good knowledge on the species life-cycle is also of great interest when the geochemistry of fossils are examined because it allows estimation of the time of the year when the valves calcified. As a consequence, it is possible to assess seasonal variation by examining the geochemistry of different species. The fractionation factors established for oxygen isotopes are necessary to interpret oxygen isotope compositions of ostracod fossils in terms of water isotopic composition and/or water temperature. This also holds true for trace-element partitioning coefficients. Therefore, a unique calibration dataset is now available to interpret past variations of ostracod fossil assemblages and geochemical data in terms of their palaeoenvironmental conditions.

In addition, in vitro laboratory experiments may further constrain which factors control the ostracod valve geochemistry. The possibility to change the chemical composition of water among the different experimental batches would permit a confirmation that oxygen isotope vital effects are dependent on chemical composition of water and to assess to which extent this can vary. This is particularly required for palaeoclimatic studies based on ostracod oxygen isotope compositions because the primordial assumption of this approach is that the oxygen isotope vital effect is constant through time. However, if lake water chemistry changed dramatically over time, the ostracod oxygen isotopic record might be biased by a change of the oxygen vital effect. This would regrettably lead to erroneous palaeoclimatic interpretations.

The present results also reveal the need to study in detail biomineralisation processes in ostracods as well as the influence of the latter on the valve geochemistry. In the present thesis, the discussion of the results showed that there might be a relationship between biomineralisation processes, valve structures and shell geochemistry. Results from previous studies and the present thesis revealed that these mechanisms are mostly similar within the same subfamily but vary significantly among the different families. A closer inspection of valve structure effectuated on species belonging to different families coupled with information on valve geochemistry obtained during this thesis might reveal interesting links between biomineralisation processes and valve geochemistry. This approach may also help us to understand which mechanisms lead to non-equilibrium isotope fractionation and which control trace-elements partitioning.

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Environmental and Biological Controls on the Geochemistry ($\delta^{18}O$, $\delta^{13}C$, Mg/Ca, and Sr/Ca) of Living Ostracods from Lake Geneva

THESIS APPENDIXES

Laurent Decrouy

Jury:

Prof. Klaus Holliger,	**Président du Jury**
Prof. Torsten Vennemann,	**Directeur de thèse**
Dr. Daniel Ariztegui,	**Expert externe**
Prof. Patrick De Deckker,	**Expert externe**
Prof. Jonathan Holmes,	**Expert externe**
Prof. Antje Schwalb,	**Expert externe**

LAUSANNE
2009

APPENDIX I

Candona candida

Candona neglecta

Fabaeformiscandona caudata

Pseudocandona compressa

Cypria ophtalmica forma *lacustris*

Ilycypris sp.

Prionocypris zenkeri

Herpetocypris reptans

Isocypris beauchampi

Cypridopsis vidua

Plesiocypridopsis & Potamocypris

Limnocythere inopinata

Limnocytherina sanctipatricii

Cytherissa lacustris

Cores LEBC

Candona candida

(O.F. Müller, 1776)

Candona candida is only found at 13 and 33 m depths with a population density (sum A-4 to Ad) of 490 and 290 Ind/m^2, respectively; representing 2.5 and 3.1 % of the entire ostracod fauna (Fig. 3.7).

C. candida produces one generation per year. At 13 m depth, A-4 juveniles appear during April and develop rapidly to reach instar A-2 in July and August. Development stops during the next three

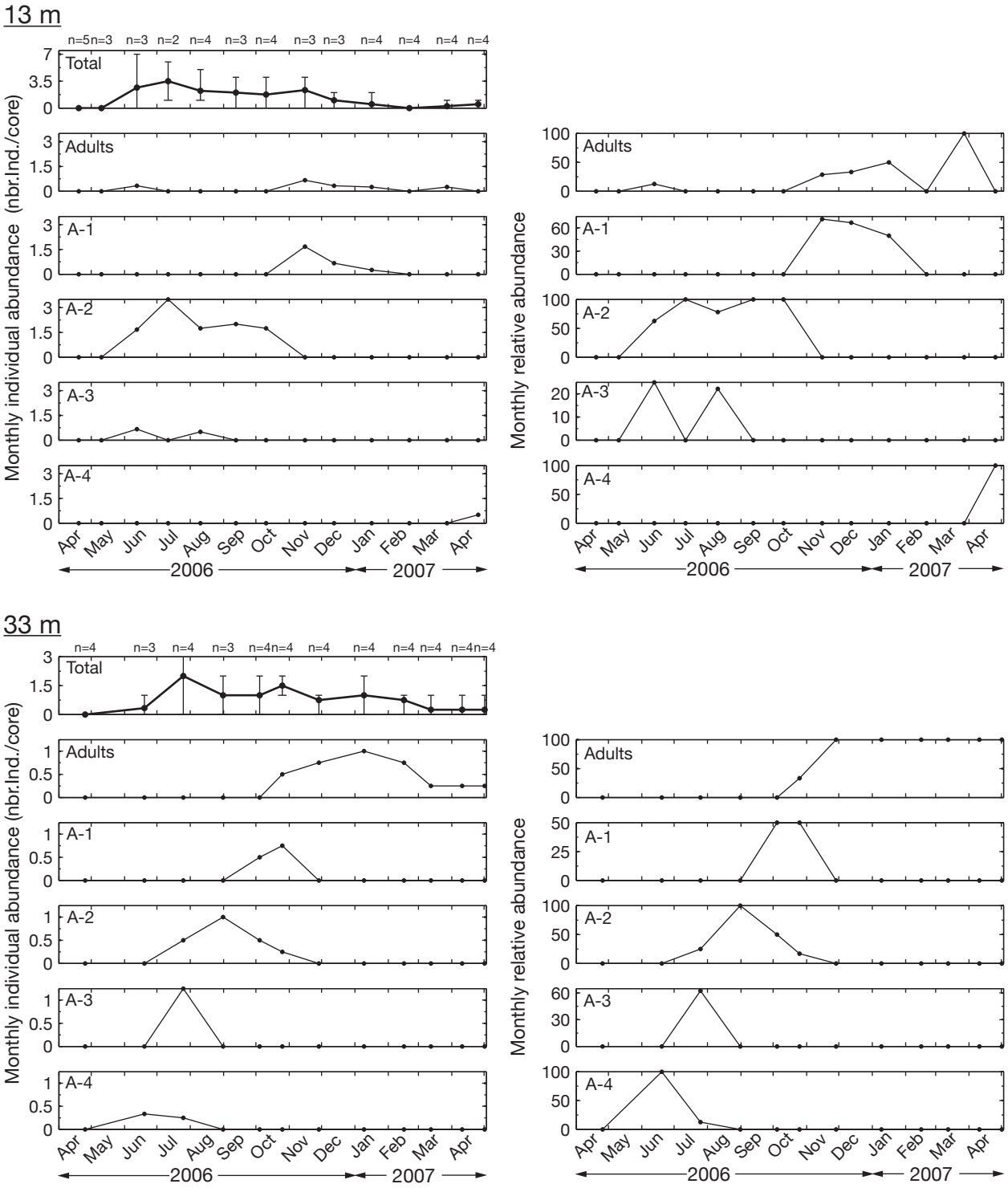

FIGURE AI.*Cc*.1
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Candona candida* at 13 and 33 m water depths.

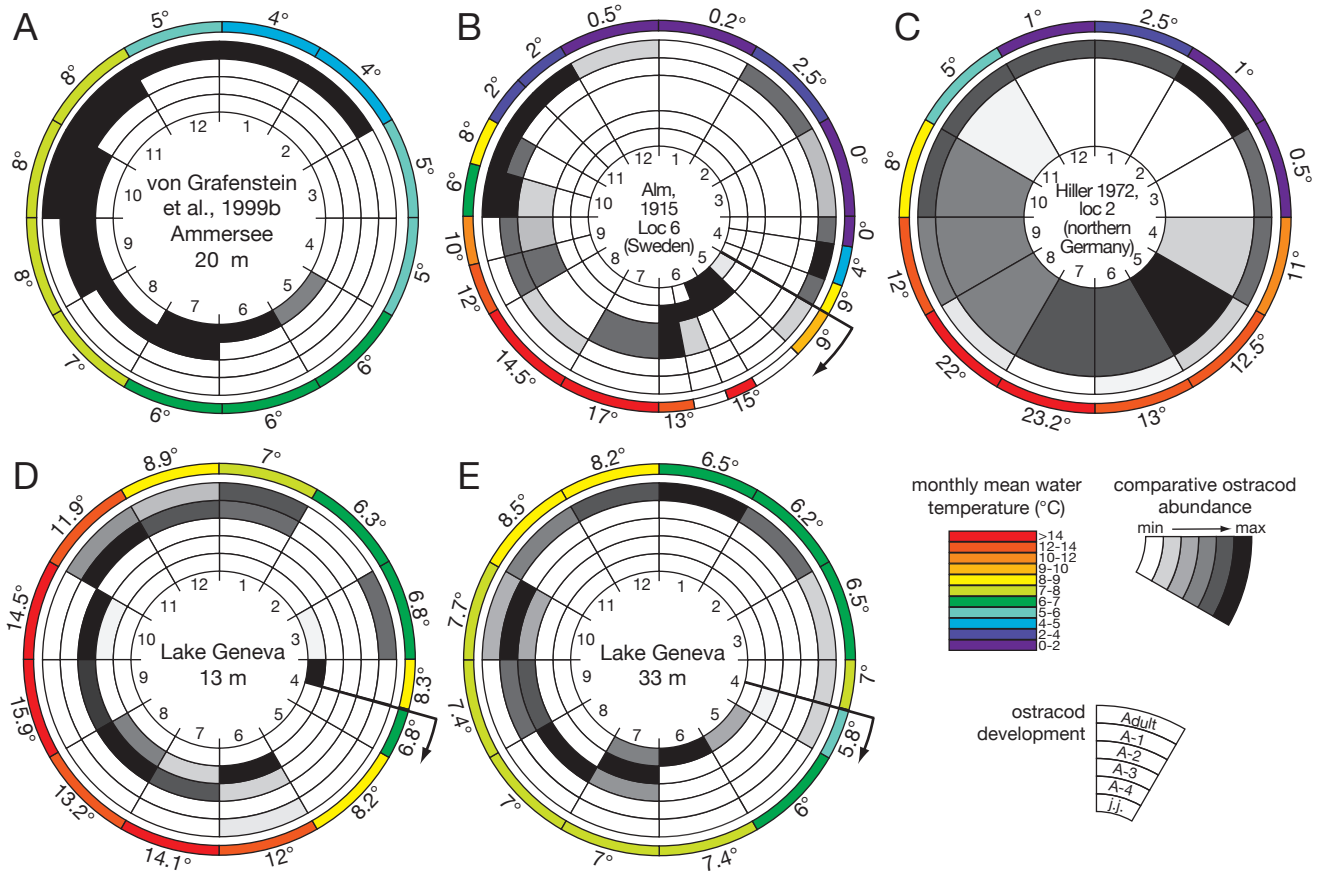

FIGURE AI.*Cc*.2
Life-cycles of *Candona candida* in different localities illustrated with SOWM. Data from: von Grafenstein et al., 1999b (A); Alm, 1915 (B); Hiller, 1972 (C); and present study (D & E).

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months and resumes in November and December as monthly water temperature decreases to less than 12°C. Moulting to adult stage occurs from November to January and last adults are found in March. At 33 m depths, development of the younger juveniles is slower and A-4 instars are found only in May. However, water temperature is fairly constant at this depth and juveniles can develop continuously without a diapause. Consequently, adulthood is already reached in October. Adults then survive for several months and living specimens can be collected until April (Fig. 3.8).

As this species is rather rare, the data of penetration depth are poor and may not be representative. Generally though, specimens seem not to burrow into the sediment and most of the specimens are found in the top half-centimetre of the sediment at the 13 m depth sampling site. At 33 m depth, specimens may penetrate slightly deeper into the sediment but data are too scarce to rigorously confirm this observation (Fig. 3.10).

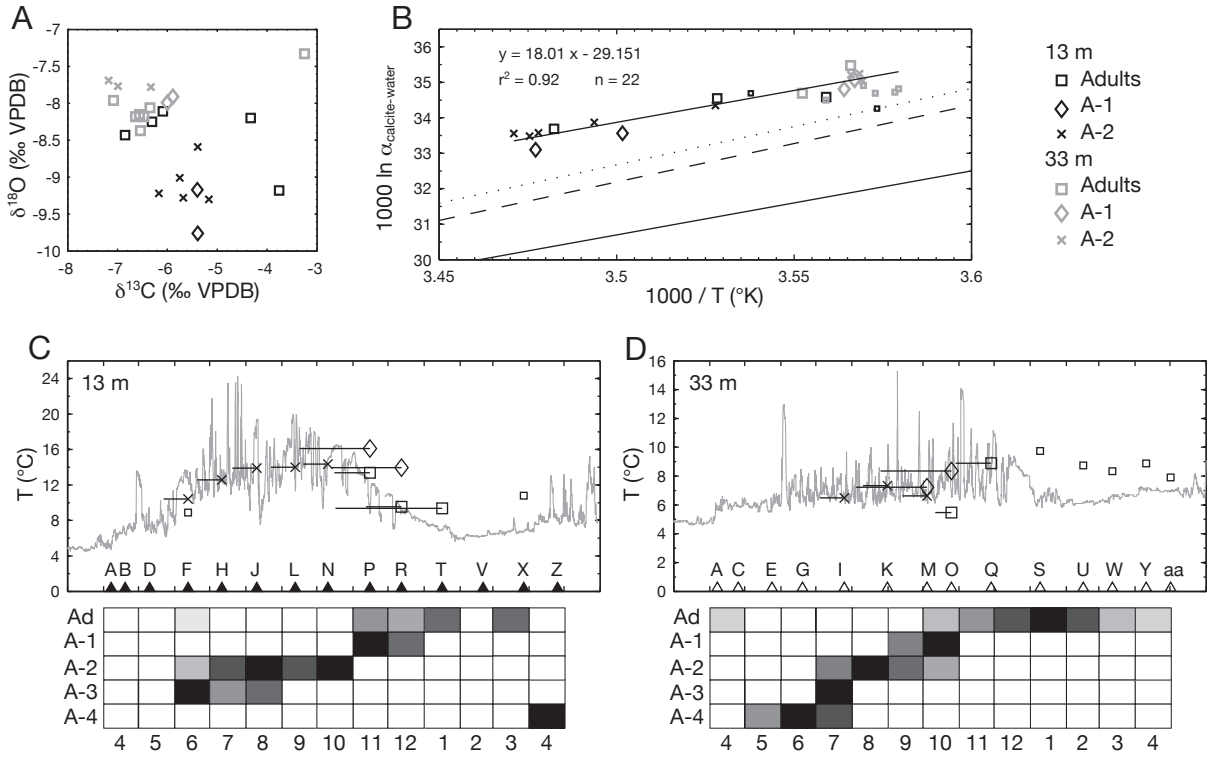

FIGURE AI.*Cc*.3
Oxygen isotope compositions of *Candona candida* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle at 13 m water depth (C); same as for C but at 33 m water depth (D).

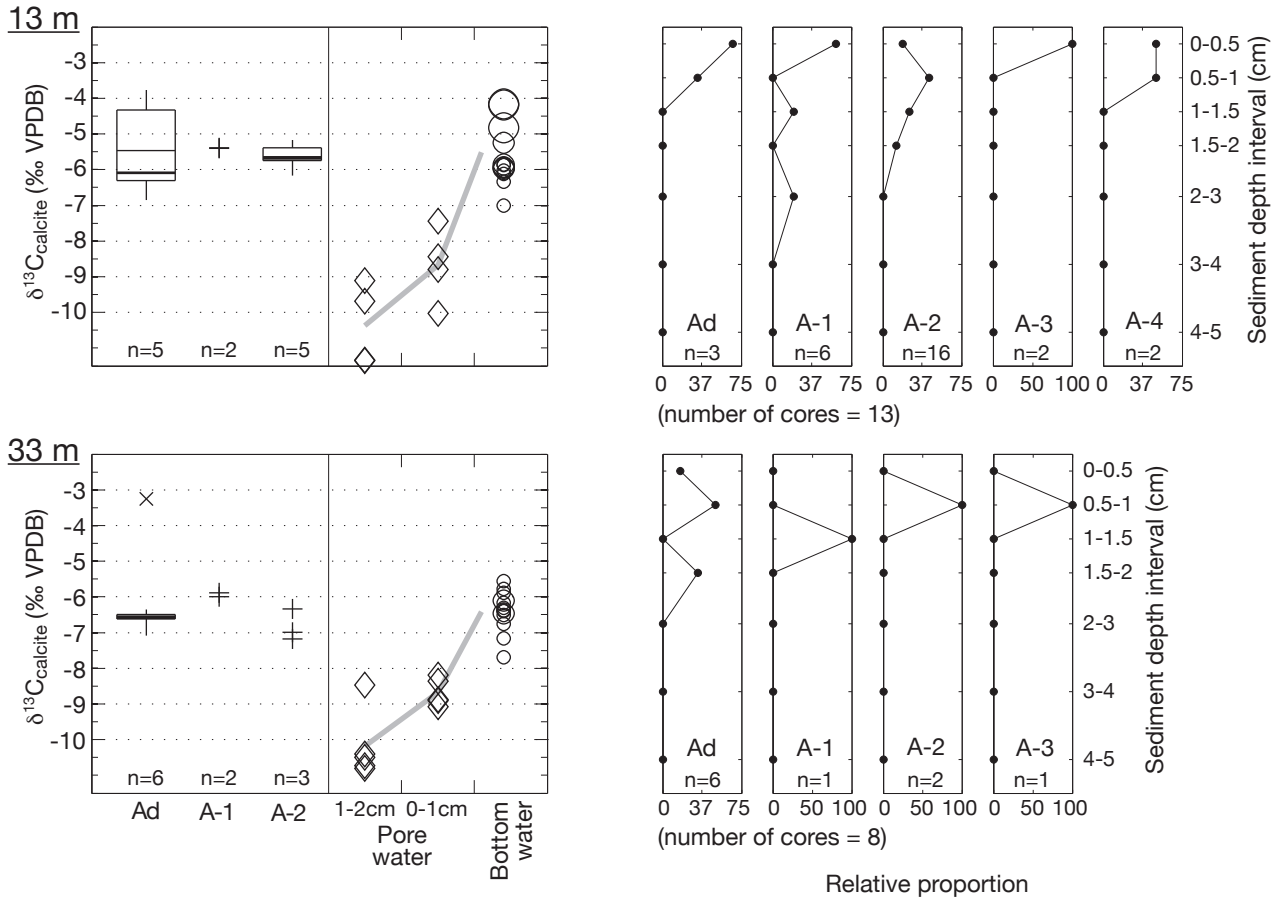

FIGURE AI.*Cc*.4
On the left side: carbon isotope compositions of *Candona candida* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 13 and 33 m water depths. On the right side: observed sediment penetration depths of *Candona candida* at 13 and 33 m water depths.

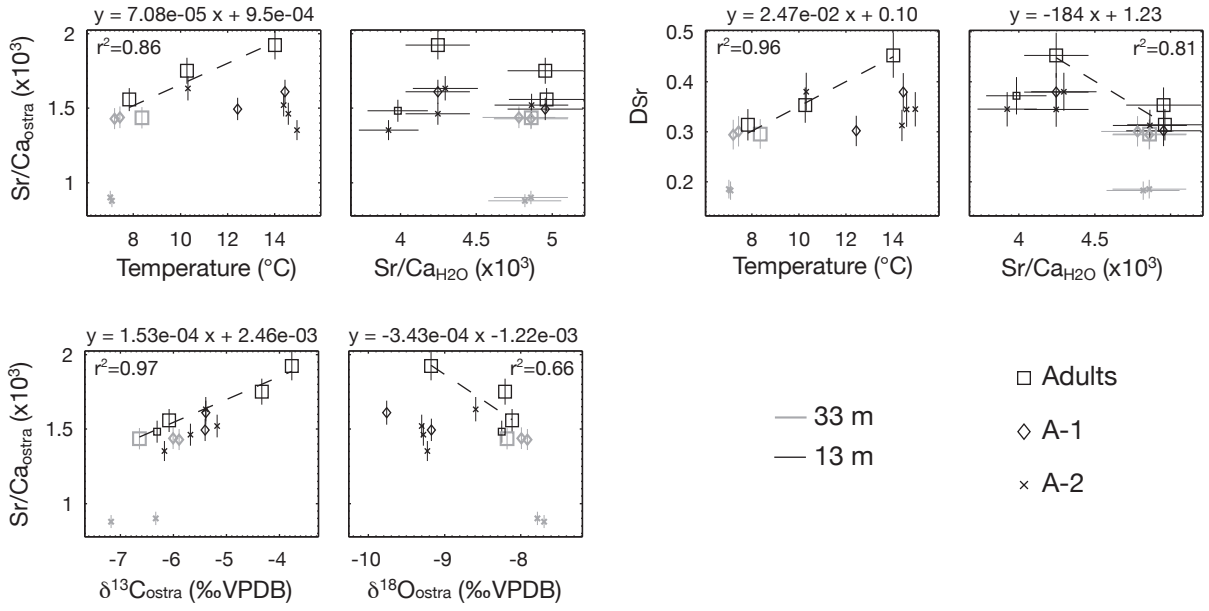

FIGURE AI.*Cc*.5
Sr/Ca and D_{Sr} of *Candona candida* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Candona neglecta

Sars, 1887

Bathymetric distribution, population density, and life history of *C. neglecta* have already been discussed in detailed in a companion paper (*Chapter III-1*). Only the most important characteristics are presented here.

C. neglecta is found in the sublittoral zones down to the deepest part of the basin. Population density (sum A-4 to adult) is high at 13 and 70 m depth, with 2800 and 2700 Ind/m^2 respectively and slightly lower at 33

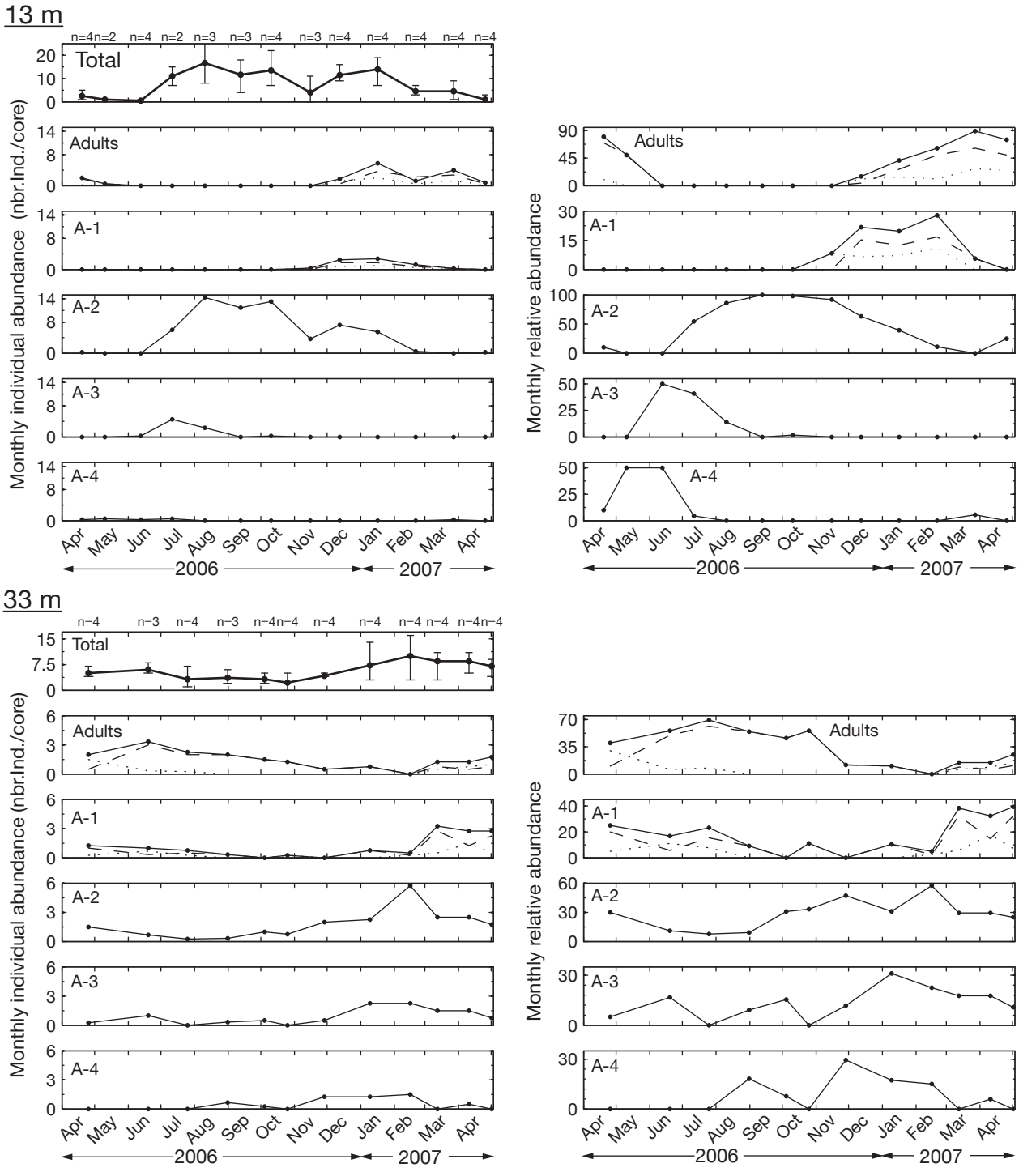

FIGURE AI.*Cn*.1a
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Candona neglecta* at 13 and 33 m water depths. Dashed lines stand for females, dotted lines for males.

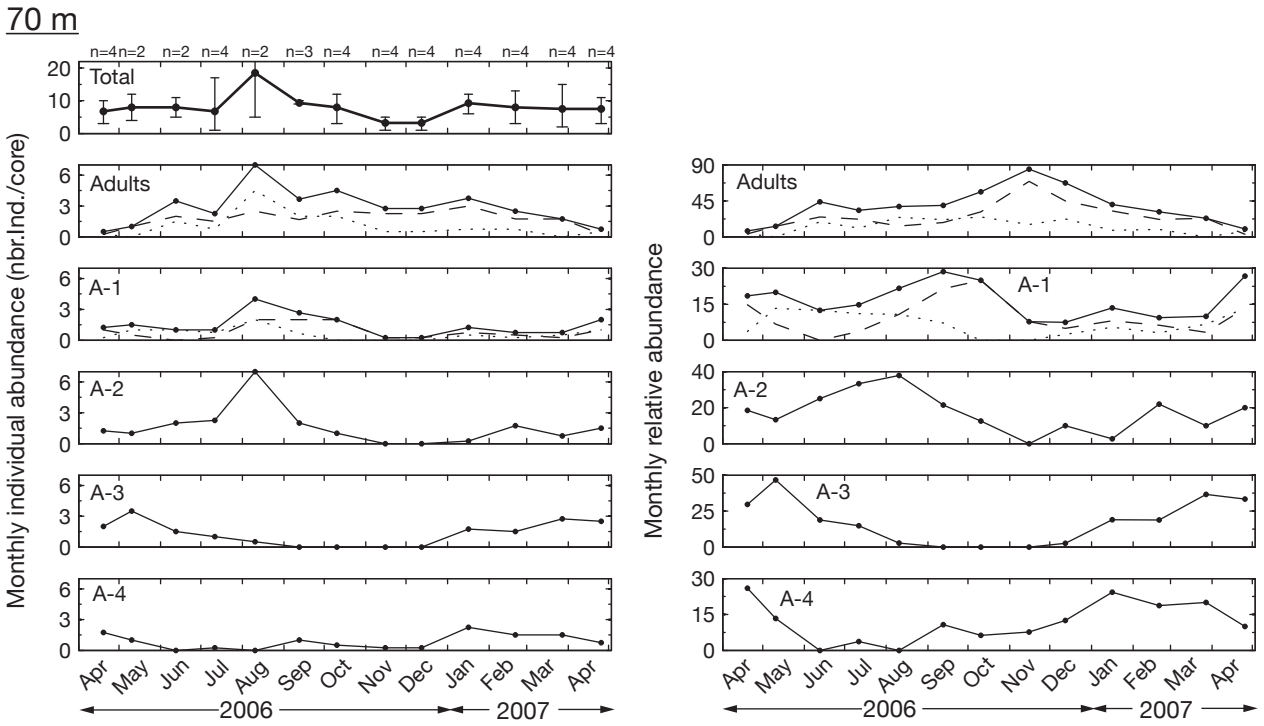

FIGURE AI.*Cn*.1b
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Candona neglecta* at 70 m water depth. Dashed lines stand for females, dotted lines for males.

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m with 2200 Ind/m^2, which represent 14, 24, and 27 % of the entire ostracod fauna at 13, 33, and 70 m depth, respectively (Fig. 3.7).

Development is different at the three depths. At 13 m, *C. neglecta* develops in approximately the same way as *C. candida*. One generation is produced per year, with a diapause during the warmest month and maturation during winter. At 33 m depth, development occurs over a longer period. A-4 instars are found from mid-summer to mid-winter and maturity is reached from early spring to mid-summer. Adult females survive until mid-winter. At 70 m, the population seems to have two groups of individuals developing separately, one reaches maturity during the end of spring and early summer, the other in autumn. It is not clear if the two groups are two different cohorts or if the two groups represent individuals of only one cohort with two different developments (Fig. 3.8).

C. neglecta is an active dweller. Sediment penetration depth increases with water depth. At 13 m depths, approximately 2/3 of the population, taking all instars together, were found in the first centimetre of the sediment, and 1/3 in the half-centimetre below. At 33 m, about 2/3 of the specimens were found between 0.5 and 1.5 cm within the sediment; the rest of the specimens were found in the top half-centimetre and down to 3 cm. At 70 m depth, 3/4 of the adults and A-1 instars are found between 0.5 to 2 cm, A-2 specimens are homogeneously distributed between 0.5 and 3 cm, most of A-3 specimens were found between 0.5 and 1 cm, the rest 0.5 cm below. In general, adults can be found slightly deeper in the sediment compared to juveniles (Fig. 3.10).

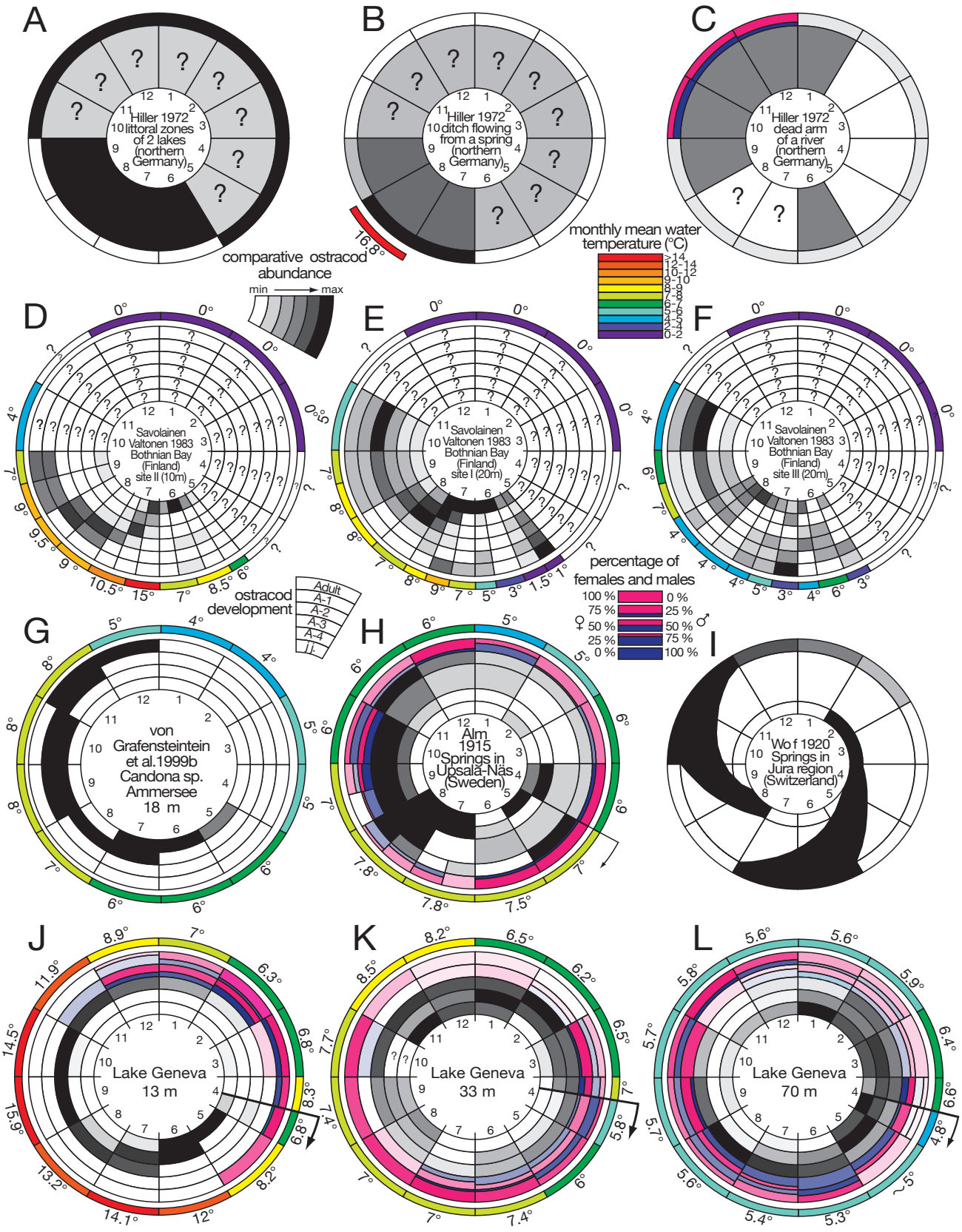

FIGURE AI.*Cn*.2
Life-cycles of *Candona neglecta* in different localities illustrated with SOWM. Data from: Hiller, 1972 (A, B, and C); Savolainen and Valtonen, 1983(D, E, and F); von Grafenstein et al., 1999b (G); Alm, 1915 (H); Wolf, 1920 (I); and present study (J, K, and L).

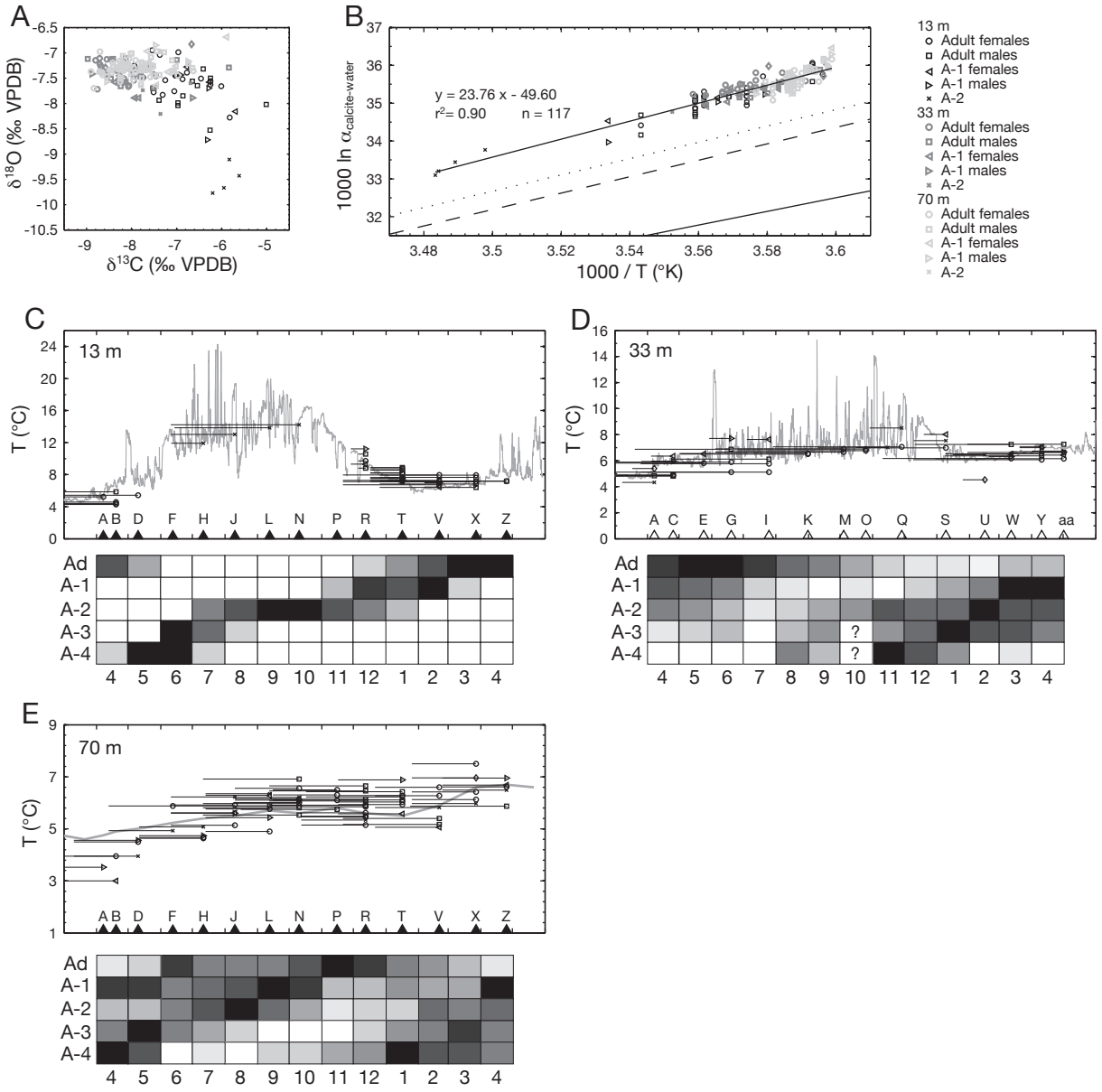

FIGURE AI.*Cn*.3
Oxygen isotope compositions of *Candona neglecta* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle at 13 m water depth (C); same as for C but at 33 m water depth (D); same as C but at 70 m water depth (E).

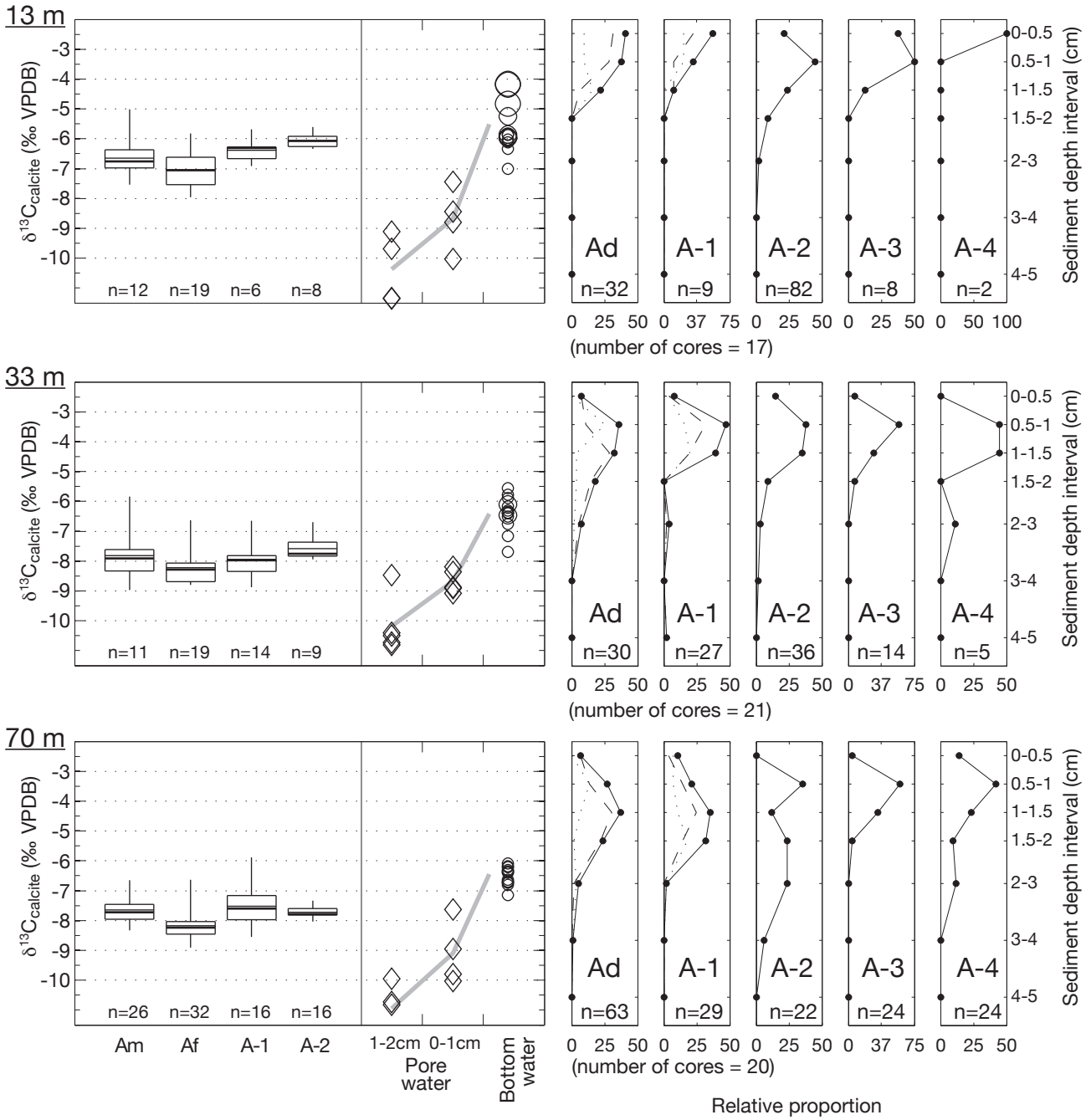

FIGURE AI.*Cn*.4
On the left side: carbon isotope compositions of *Candona neglecta* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 13, 33, and 70 m water depths. On the right side: observed sediment penetration depths of *Candona neglecta* at 13, 33, and 70 m water depths. Dashed lines stand for females, dotted lines for males.

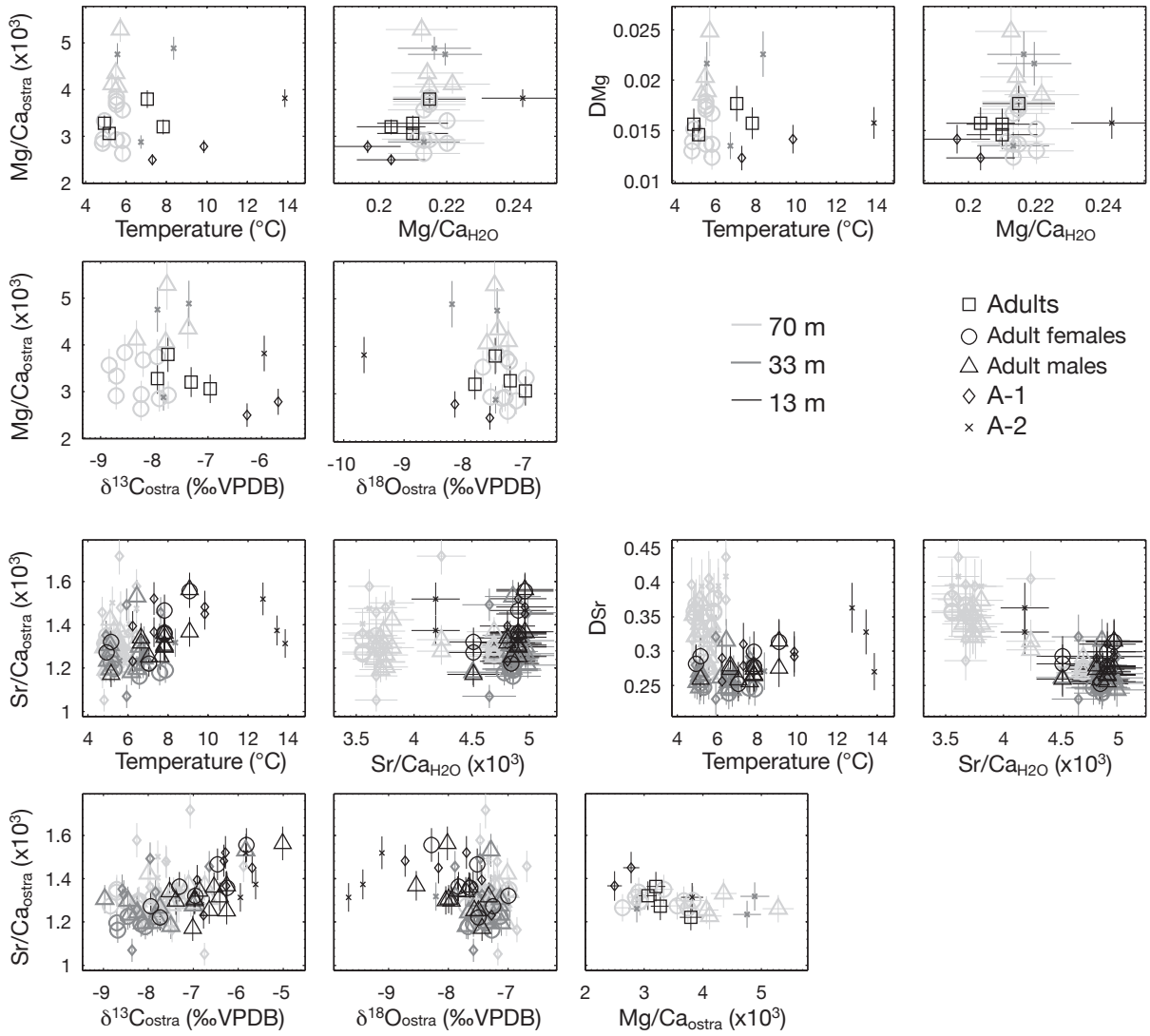

FIGURE AI.*Cn*.5
Sr/Ca, D_{Sr}, Mg/Ca, and D_{Mg} of *Candona neglecta* valves versus water temperature, Sr/Ca and Mg/Ca ratios of water and C- and O- isotope compositions of the valves.

Fabaeformiscandona caudata

(Kaufmann, 1900)

Fabaeformiscandona caudata was found at 13 m depths only, with 2000 Ind/m^2 (A-4 to adult) recovered, representing 6.8 % of the entire ostracod population (Fig. 3.7).

Development of *F. caudata* is quite similar to the one of *C. candida*. A-4 instars appear in spring and enter the diapause during summer and autumn. Maturation occurs during the coldest period of the year. What is particular in the life history of *F. caudata* is that, even if the major part of the population follows the typical development of Candoninae at 13 m, some individuals are able to develop out of time and A-1 and adult specimens can moult during warm periods (Fig. 3.8). Oxygen isotopic compositions indicate that A-1 and adult specimens collected in June, July, August, November, December, and April moulted during the month preceding sampling, with water temperature ranging between 9 to 14°C.

F. caudata is quite an active dweller. Penetration depth is different for all instars. A-3 specimens cannot dig very deep into the sediment and 3/4 of the specimens are found in the top half centimetre, the last 1/4 is found in the half centimetre below. 90% of A-2 specimens are found between 0 and 1.5 cm, with a maximum between 0.5 and 1 cm. 90% of A-1 individuals were homogeneously distributed between 0.5 and 2 centimetres. 95% of adults were found in the first 1.5 cm, with maximum values in the first centimetre (Fig. 3.10).

Pseudocandona compressa is a typical littoral species. At 5 m depth, this species is dominant with very high specimen abundance. At 2 m depth, the population is important but does not dominate the ostracod fauna. Some living individuals were found at 13 m depths, but have certainly been reworked from the littoral during strong wave action (Fig. 3.7).

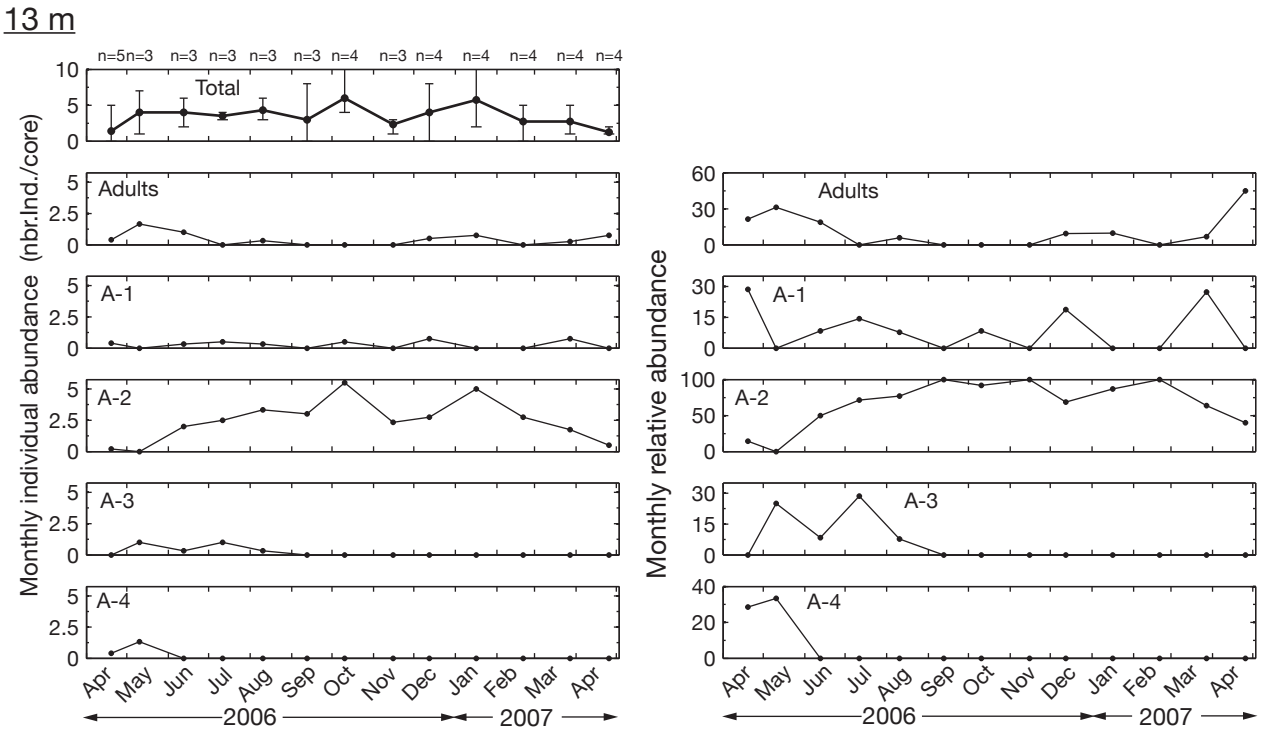

FIGURE AI.*Fc*.1
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Fabaeformiscandona caudata* at 13 m water depth.

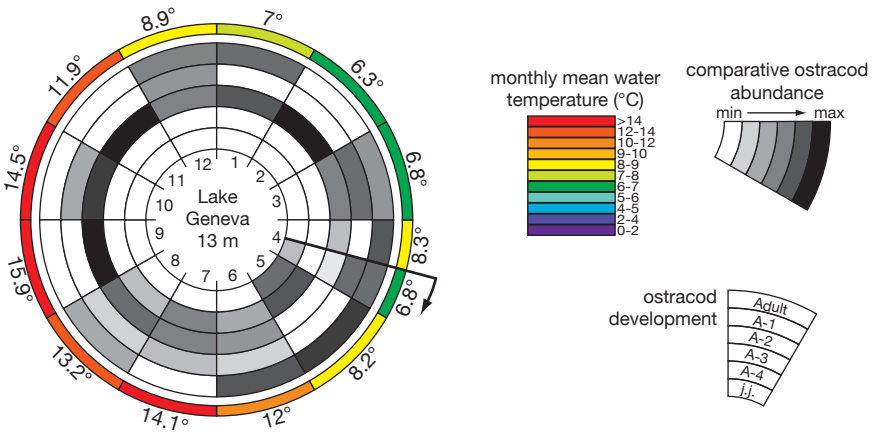

FIGURE AI.*Fc*.2
Life-cycle of *Fabaeformiscandona caudata* at 13 m water depth illustrated with SOWM.

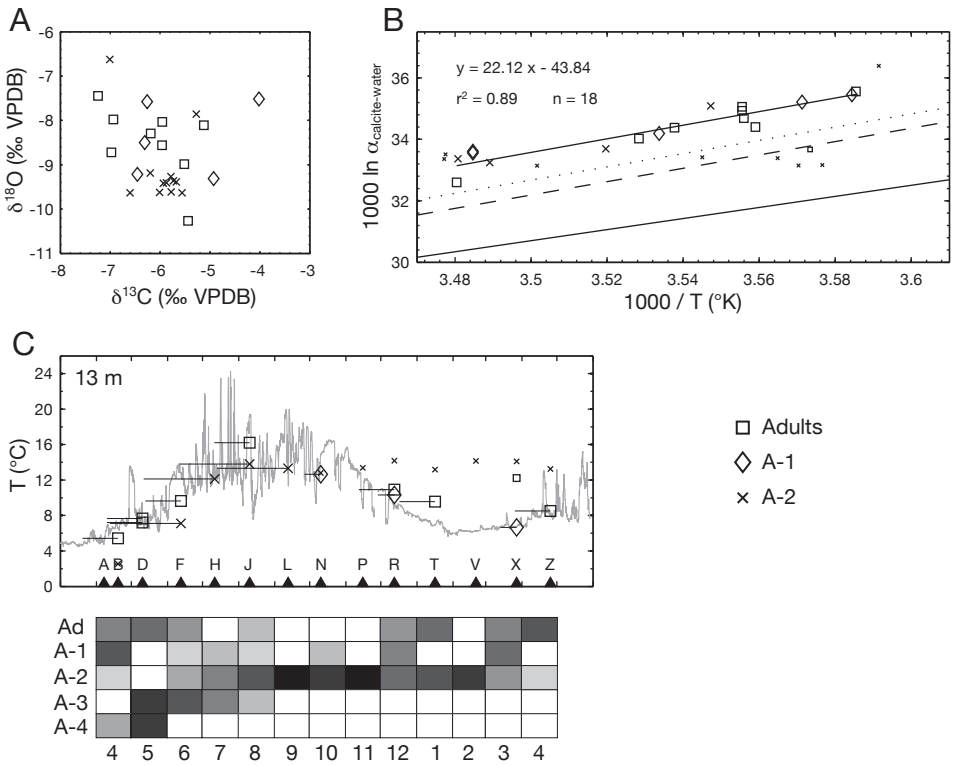

FIGURE AI.*Fc*.3
Oxygen isotope compositions of *Fabaeformiscandona caudata* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle at 13 m water depth (C).

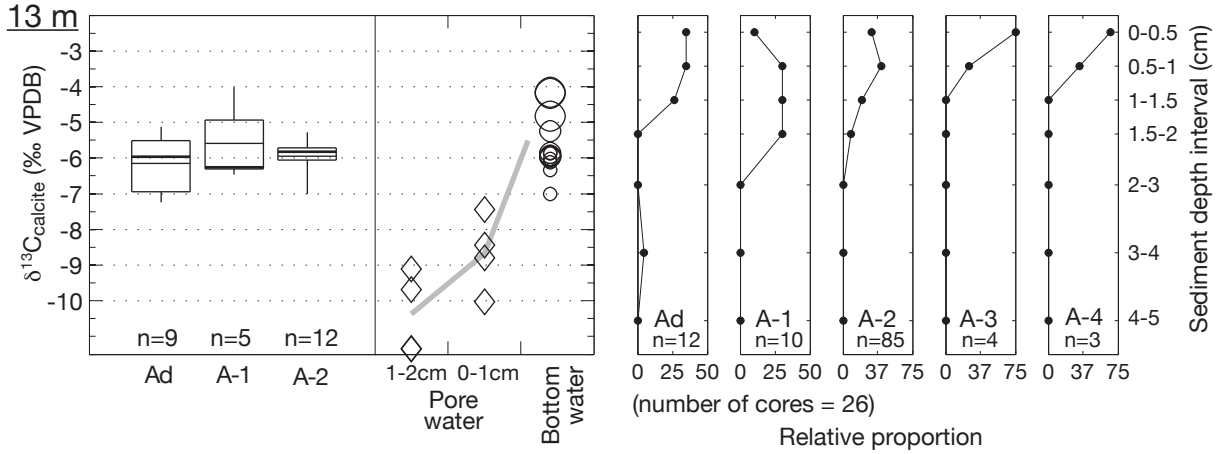

FIGURE AI.*Fc*.4
On the left side: carbon isotope compositions of *Fabaeformiscandona caudata* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 13 m water depth. On the right side: observed sediment penetration depths of *Fabaeformiscandona caudata* at 13 m water depth.

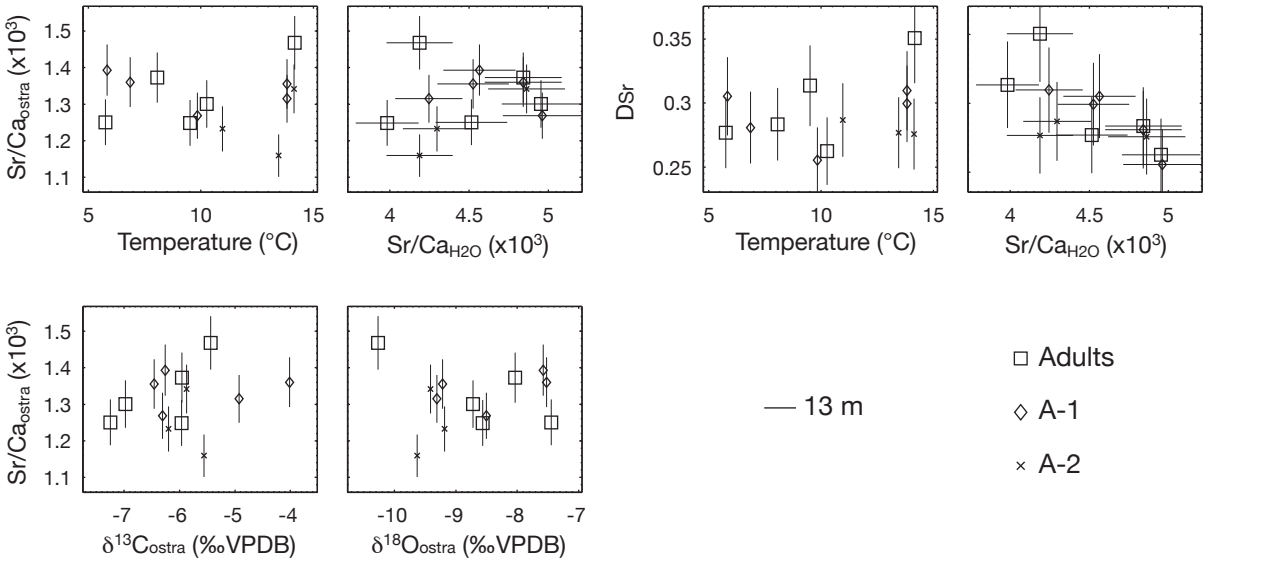

FIGURE AI.*Fc*.5
Sr/Ca and D_{Sr} of *Fabaeformiscandona caudata* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Pseudocandona compressa

(Koch, 1838)

Ps. compressa produces one generation per year. Development at 2 and 5 m depths is mostly identical. First A-3 juveniles appear in summer and all individuals moult to A-2 before autumn and hibernate in this stage (diapause). Development resumes timidly at the first increase of water temperature and increases strongly in early spring. Adults, principally females, can then survive until the end of autumn. Males dominate at the beginning of the moulting season from A-2 to A-1 and from A-1 to adult. Thereafter females outnumber males (Fig. 3.8). This variation of male:female ratio with, at first, a brief dominance of males followed by a large dominance of females has already been observed for *Ps. compressa* (Hartwig, 1901; Alm, 1915). The variation of the male:female ratio of *Ps. compressa* probably ensues from the same reproduction behaviour compared to *C. neglecta* (*Chapter III-1*).

At 2 m depth, *Ps. compressa* was largely recovered on pebbles and algae, and practically no specimens were found in the sand. At 5 m depth, most specimens were collected in the sand and few on algae and pebbles.

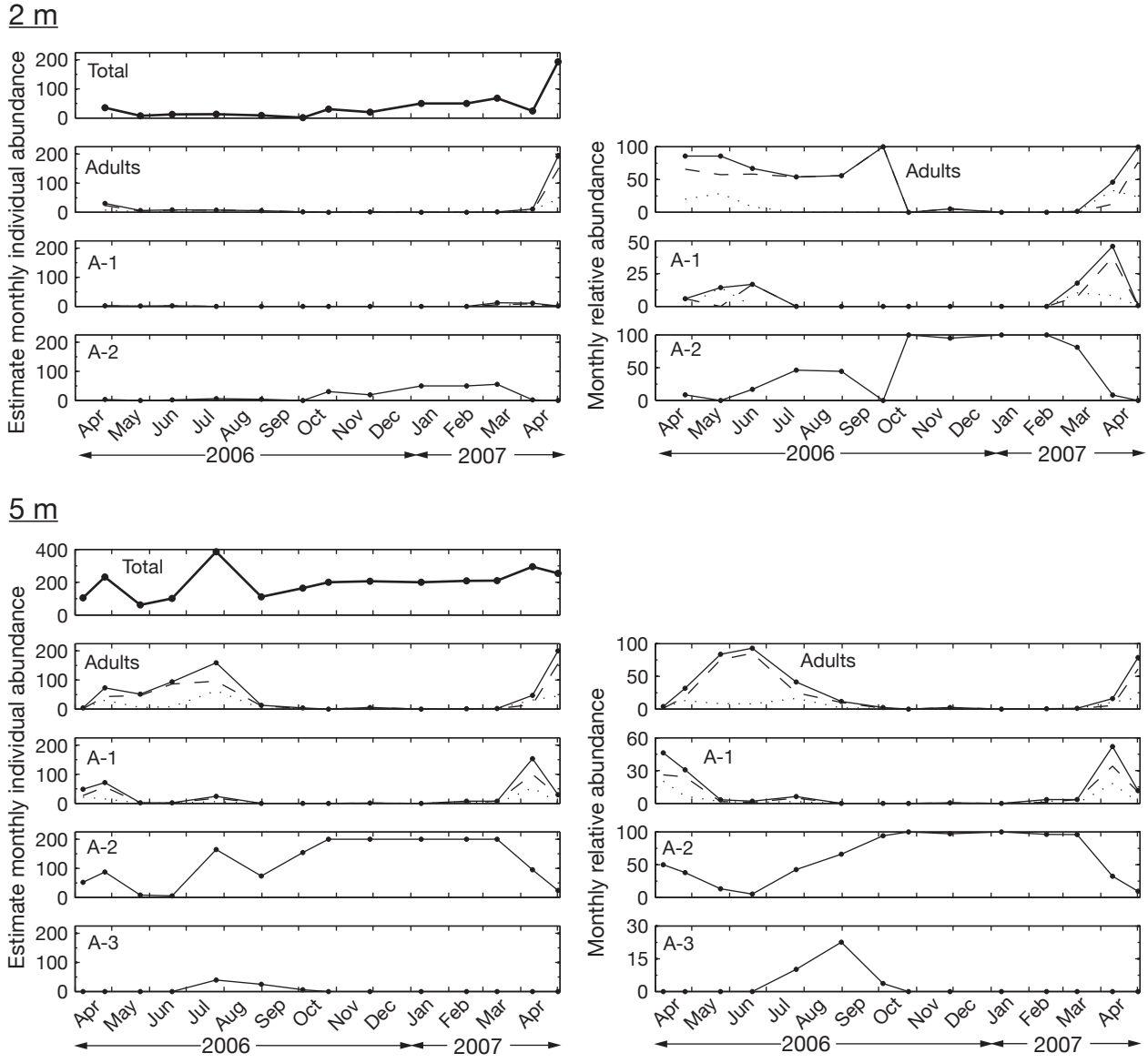

FIGURE AI.*Pc*.1
Estimated monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Pseudocandona compressa* at 2 and 5 m water depths. Dashed lines stand for females, dotted lines for males.

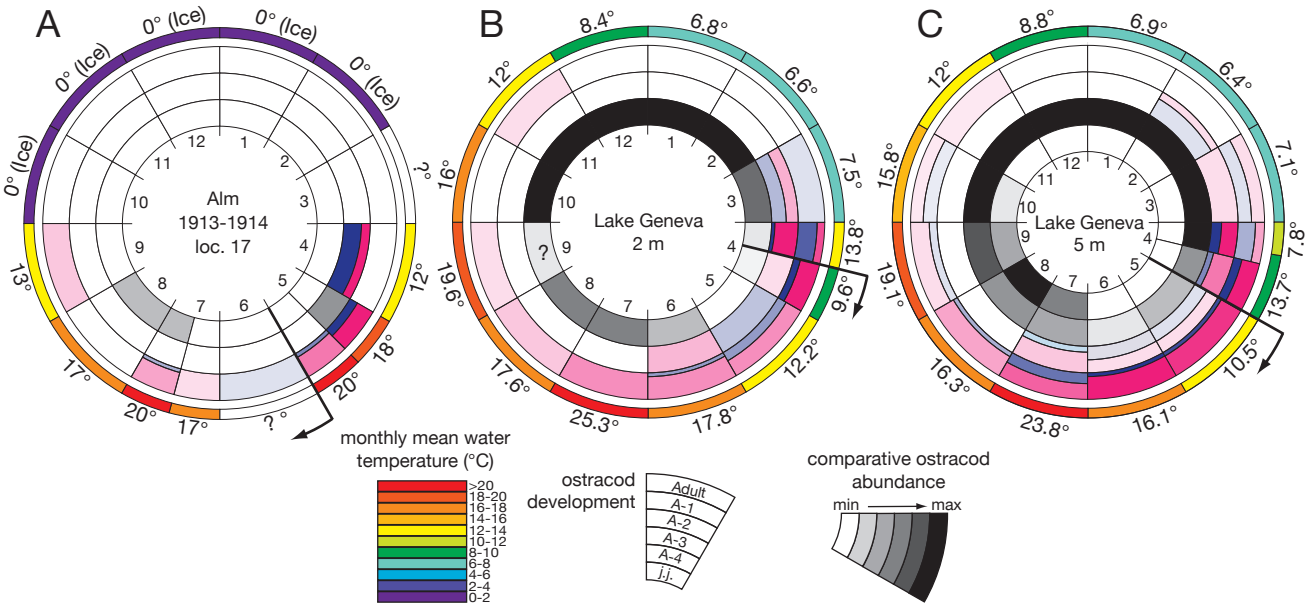

FIGURE AI.*Pc*.2
Life-cycles of *Pseudocandona compressa* in different localities illustrated with SOWM. Data from: Alm, 1915 (A); and present study (B and C).

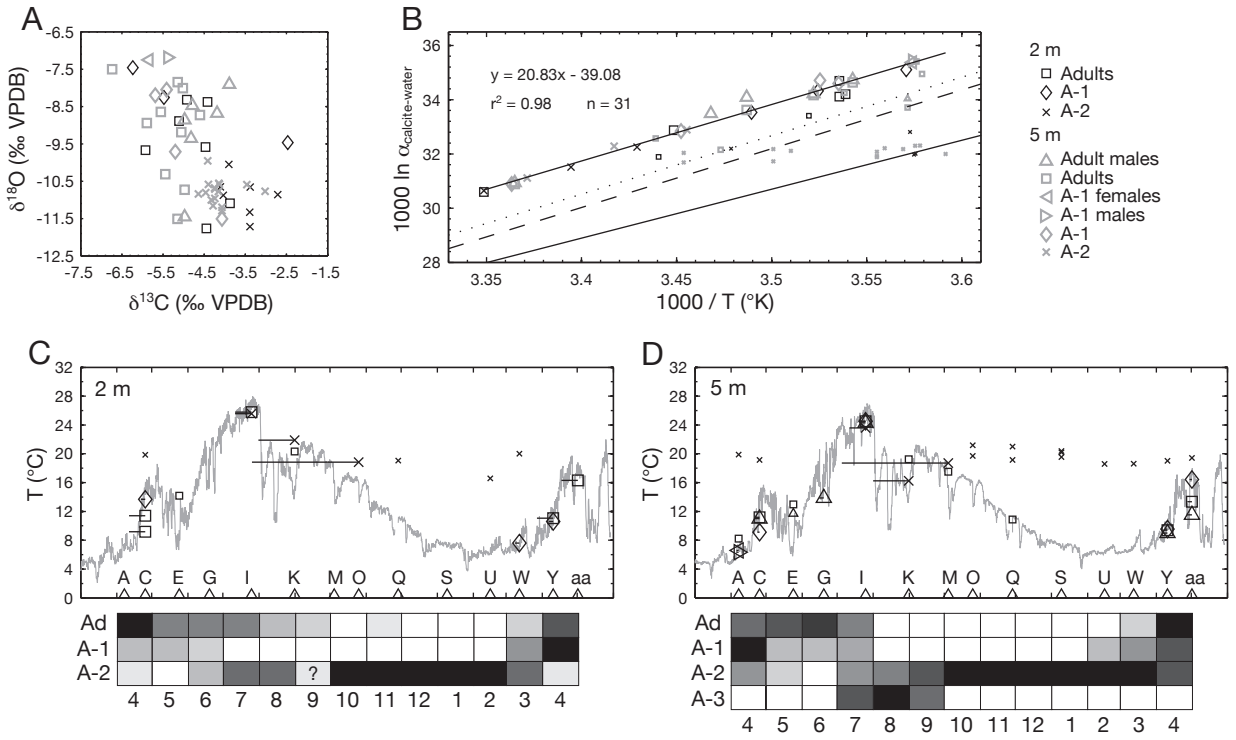

FIGURE AI.*Pc*.3
Oxygen isotope compositions of *Pseudocandona compressa* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle at 2 m water depth (C); same as for C but at 5 m water depth (D).

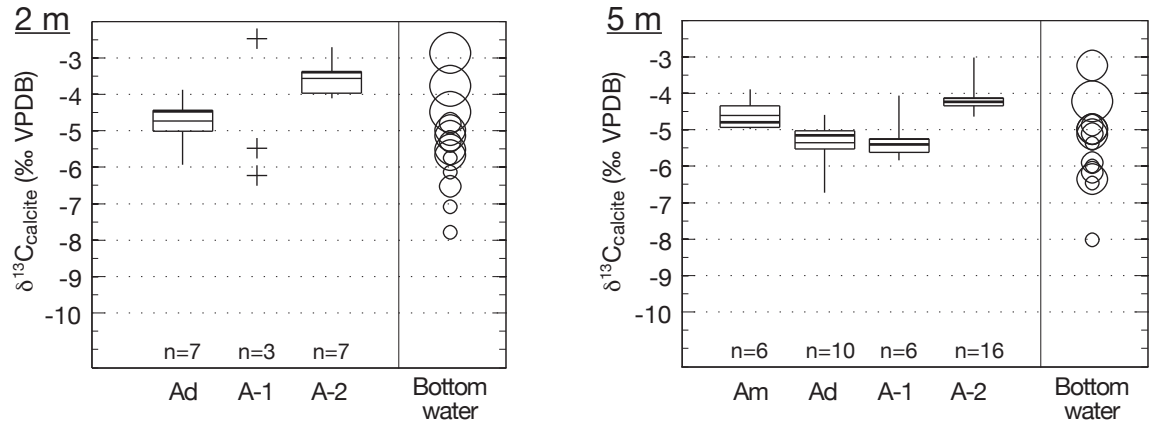

FIGURE AI.*Pc*.4
Carbon isotope compositions of *Pseudocandona compressa* valves and values for a calcite grown in equilibrium with DIC of bottom water at 2 and 5 m water depths.

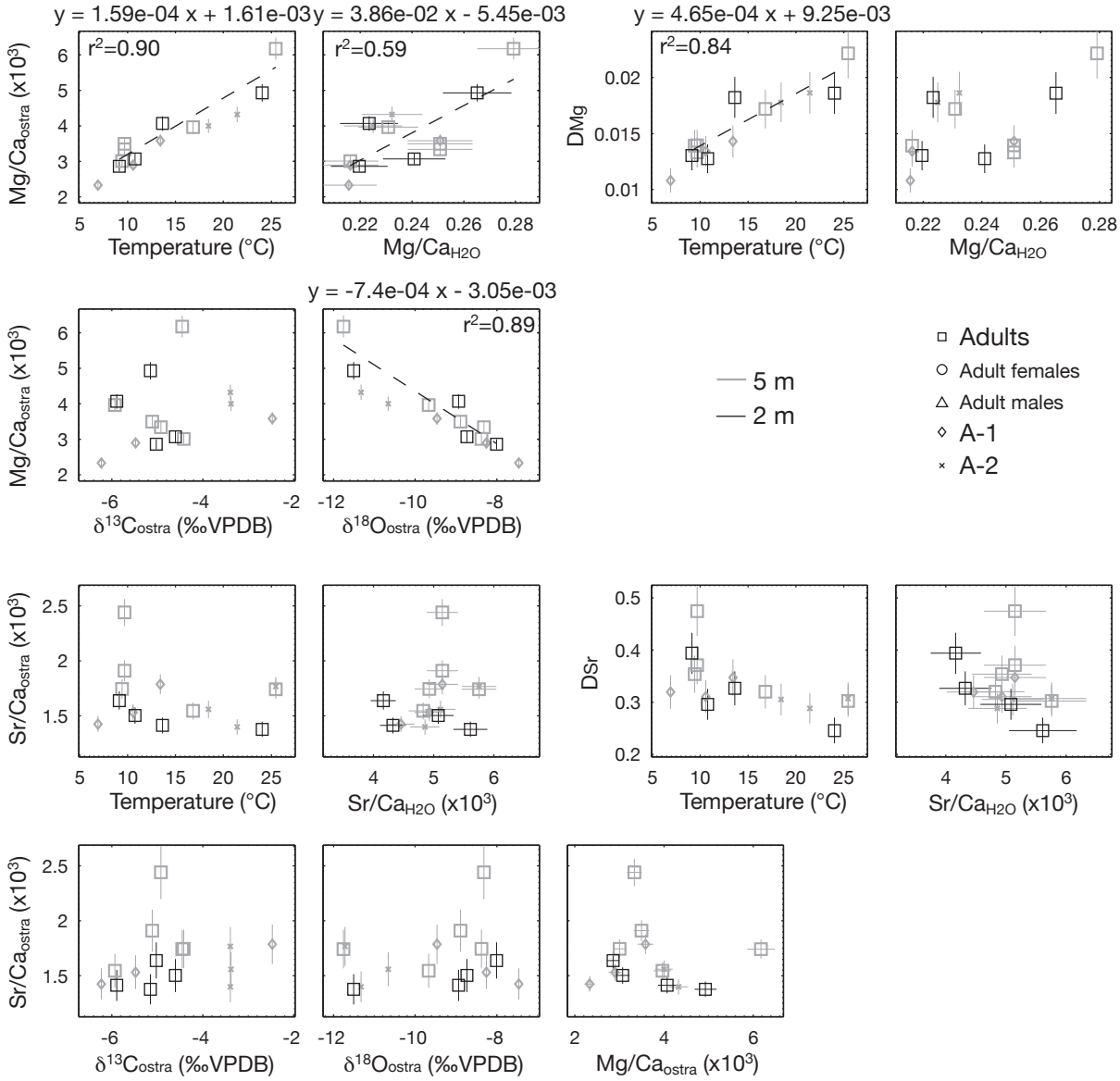

FIGURE AI.*Pc*.5
Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr} of *Pseudocandona compressa* valves versus water temperature, Mg/Ca or Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Cypria ophtalmica forma *lacustris*

(Jurine, 1820)

Cypria ophtalmica forma *lacustris* is found from 13 to 70 m depths and is thus one of the profundal species of Lake Geneva. Population density is 1100, 76, and 970 Ind/m^2, representing 5.7, 0.8, and 9.3 % of the entire population at 13, 33, and 70 m, respectively (Fig. 3.7).

Development of *C. ophtalmica* is not straightforward due to the relatively long life of the species (Meisch, 2000). Figure 3.8 illustrates that adults and juveniles are present throughout the year. At 70 m, two maxima can be seen, suggesting that the population produces two generations per year. Oxygen isotopic

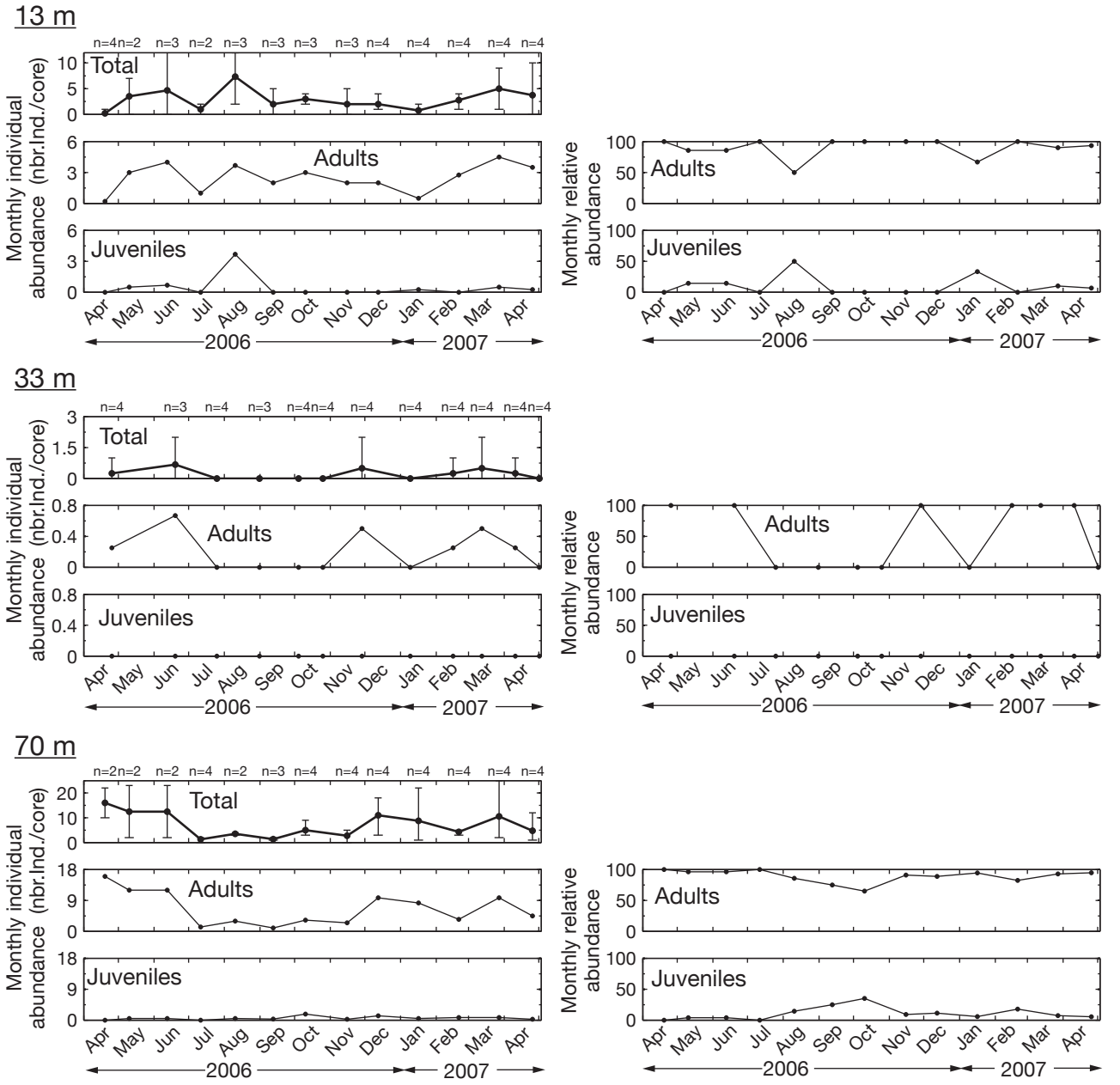

FIGURE AI.*Co*.1
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Cypria ophtalmica* at 13, 33 and 70 m water depths.

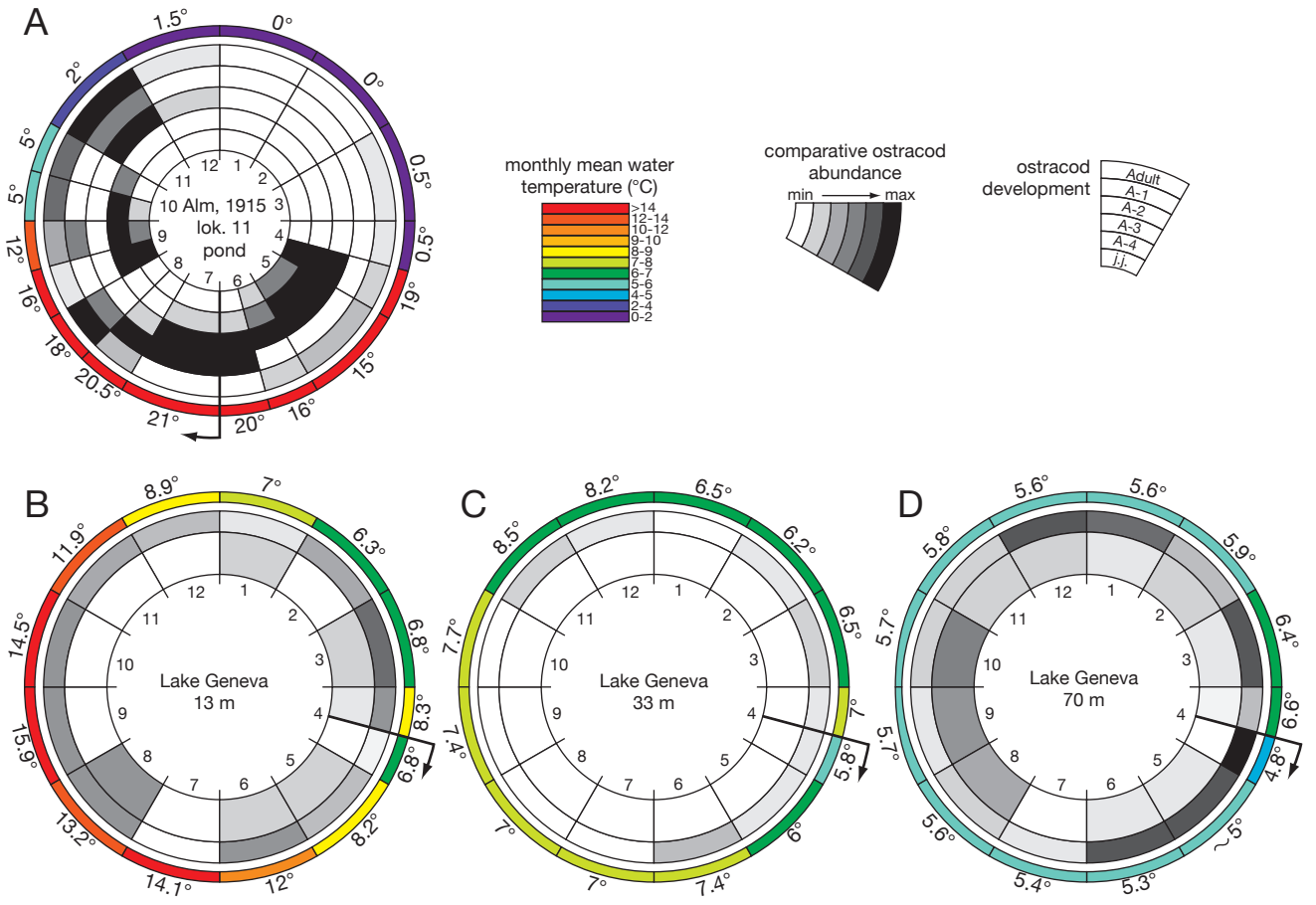

FIGURE AI.*Co*.2
Life-cycles of *Cypria ophtalmica* in different localities illustrated with SOWM. Data from: Alm, 1915 (A); and present study (B, C, and D).

compositions of the specimens collected at 13 m depths indicate that the water temperature during valve calcification varied between approximately 11 and 15 °C. *C. ophtalmica* produces, therefore, only one generation per year at 13 m depths with adults moulting from August to November.

Specimens of *C. ophtalmica* were mainly found in the top centimetre of the sediment. At 13 m, almost 60 % of the population is found in the top half centimetre, and about 30 % is found in the half-centimetre below this. No specimens were found deeper than 1.5 cm. At 70 m, penetration depth of the adults is slightly higher, with 90 % of adults found between 0 and 1.5 cm, with a maxima between 0.5 and 1 cm. Juveniles do not dig deep, and the majority of specimens are found in the top half-centimetre. Penetration depth of adults at 33 m resembles that at 70 m, but data are too scarce to be interpreted with certainty (Fig. 3.10).

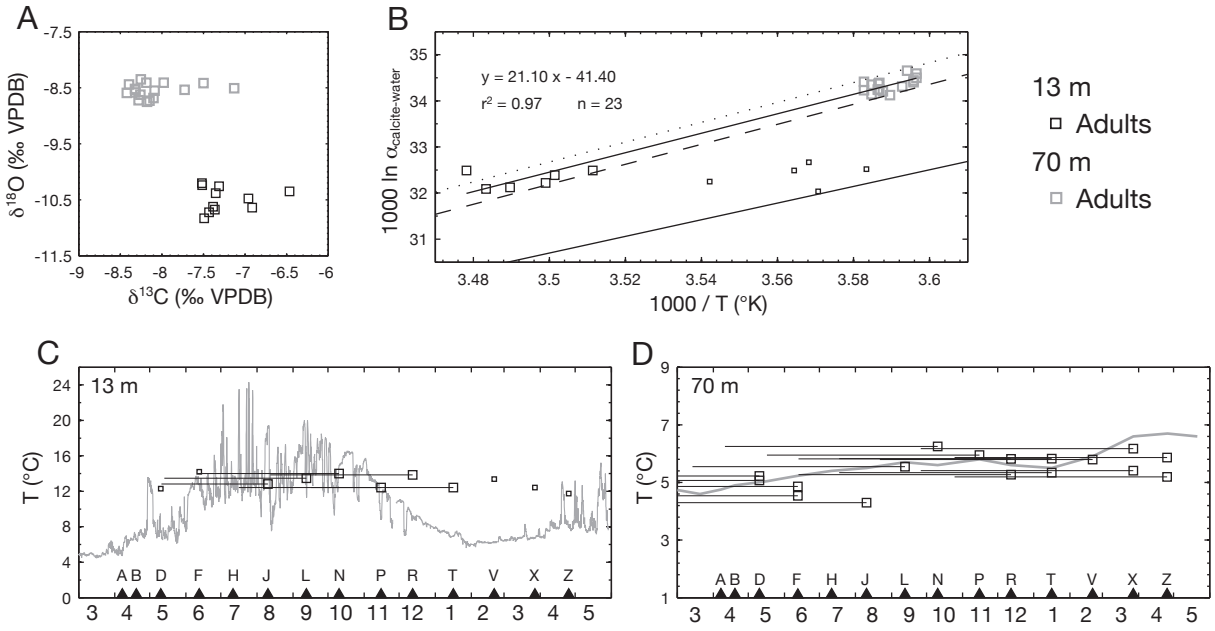

FIGURE AI.*Co*.3
Oxygen isotope compositions of *Cypria ophtalmica* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures at 13 m water depth (C); same as for C but at 70 m water depth (D).

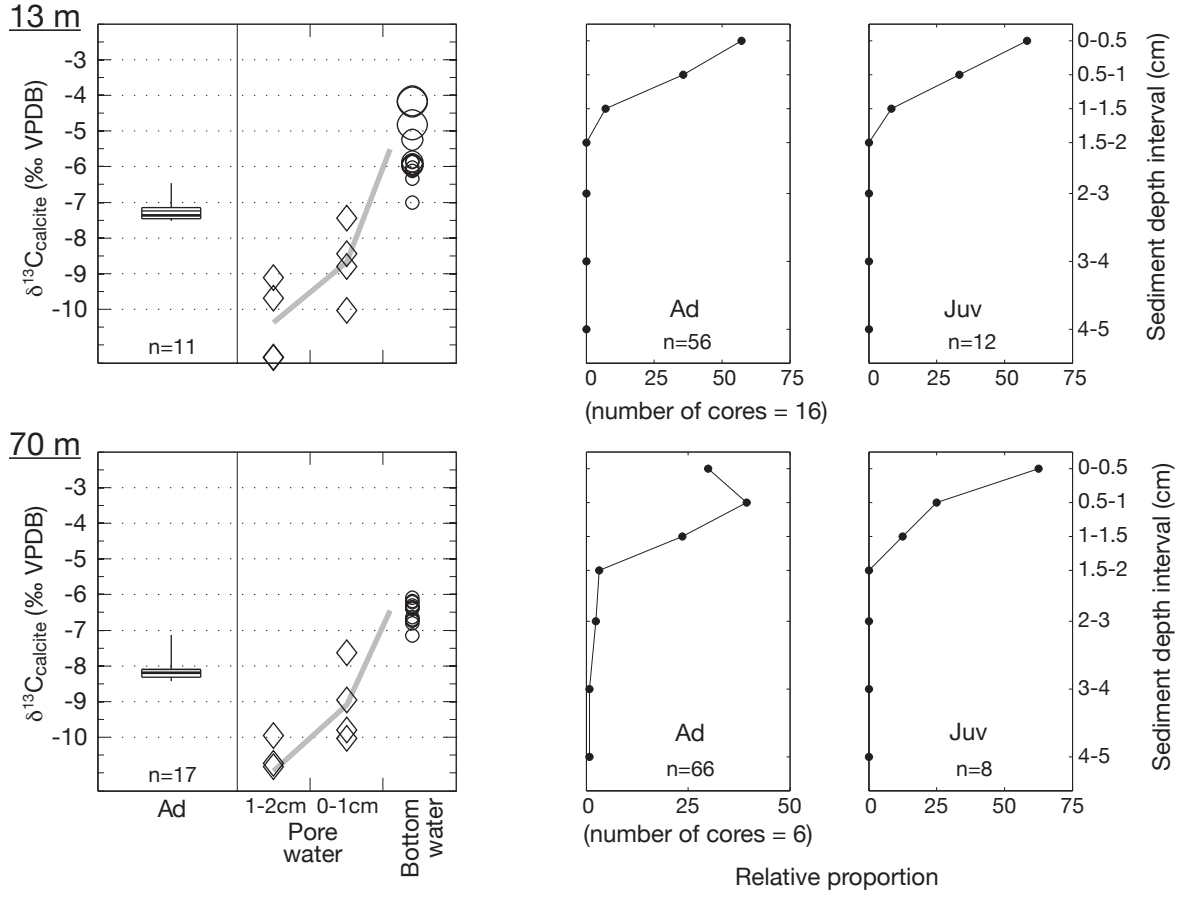

FIGURE AI.*Co*.4
On the left side: carbon isotope compositions of *Cypria ophtalmica* valves and values for a calcite grown in equilibrium with DIC of bottom water and pore water DIC at 13 and 70 m water depths. On the right side: observed sediment penetration depths of *Cypria ophtalmica* at 13 and 70 m water depths.

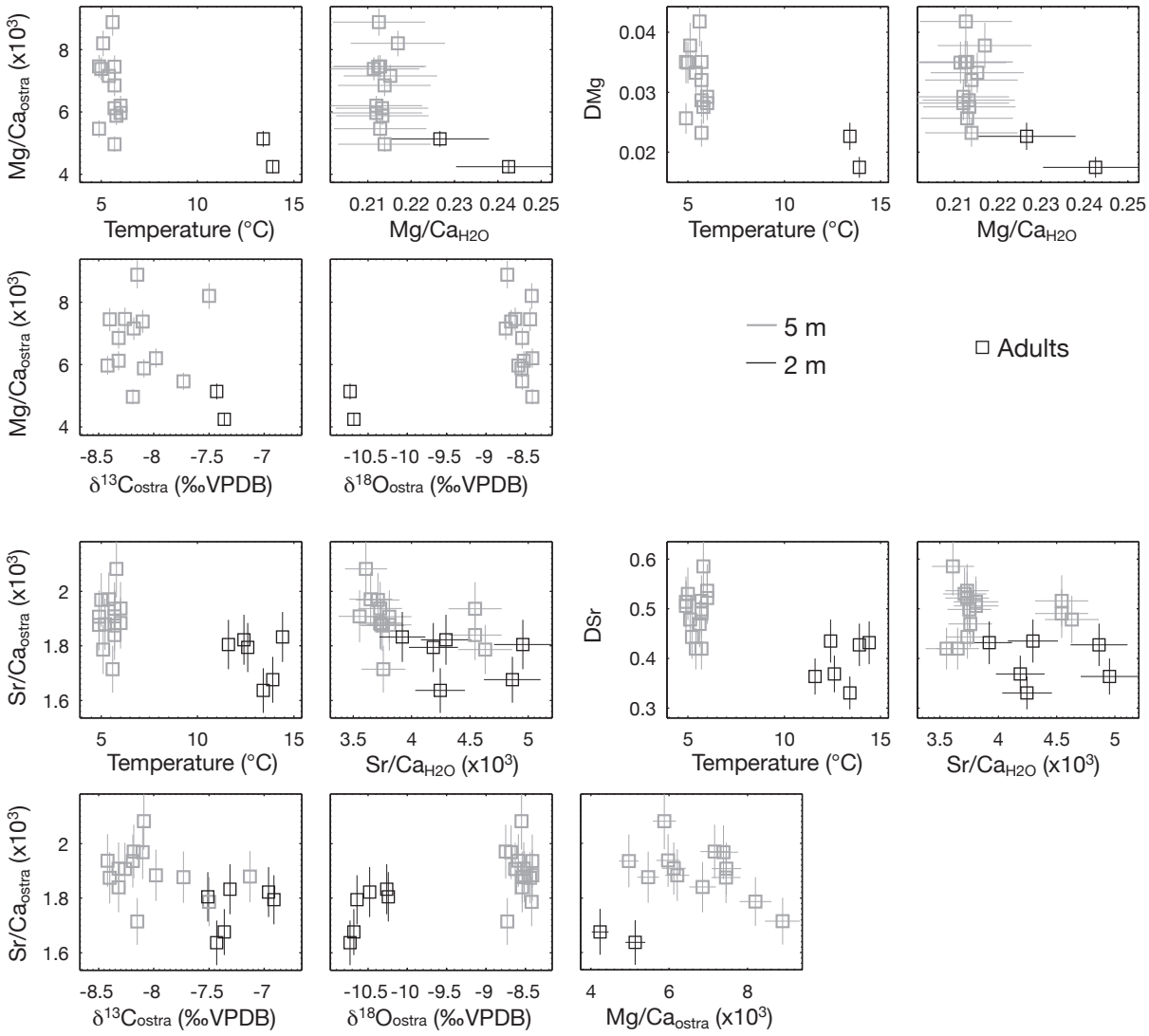

FIGURE AI.*Co*.5
Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr}, of *Cypria ophtalmica* valves versus water temperature, Mg/Ca or Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Ilycypris sp.

Species identification for these specimens was problematic. Two carapace morphologies were observed (Plate 1) but no differences could be observed on the soft parts. As these forms are very rare in Lake Geneva, identification was limited to the genus level. Only 7 specimens were found through the year at 2, 5 and 13 m depths. 2 specimens were found in May and 1 in June at 2 m, 1 in April and 1 in June at 5 m and 2 in April at 13 m depths. *Ilyocypris sp.* has only been found on pebbles at 2 m and in the sand at 5 and 13 m depths.

Prionocypris zenkeri

(Chyzer & Toth, 1858)

Prionocypris zenkeri 10 specimens (5 adults and 5 juveniles) of *P. zenkeri* were recovered at 2 and 5 m. The occurrence of this species in lakes is generally interpreted as passive import from nearby streams (Meisch, 2000). In lake Geneva, it is difficult to exclude this hypothesis. Nevertheless, the two shallow sites are far away from water inflows. Moreover, oxygen isotopic composition of the shells suggests that calcification occurred in lake water (*Chapter V-1*). In addition, both juveniles and adults were found at the same period of the year (April to July) in 2006 and 2007, suggesting that the occurrence of the animals follows a cyclic development in the zone. The specimens were recovered on pebbles and algae at 2 m and in sand at 5 m.

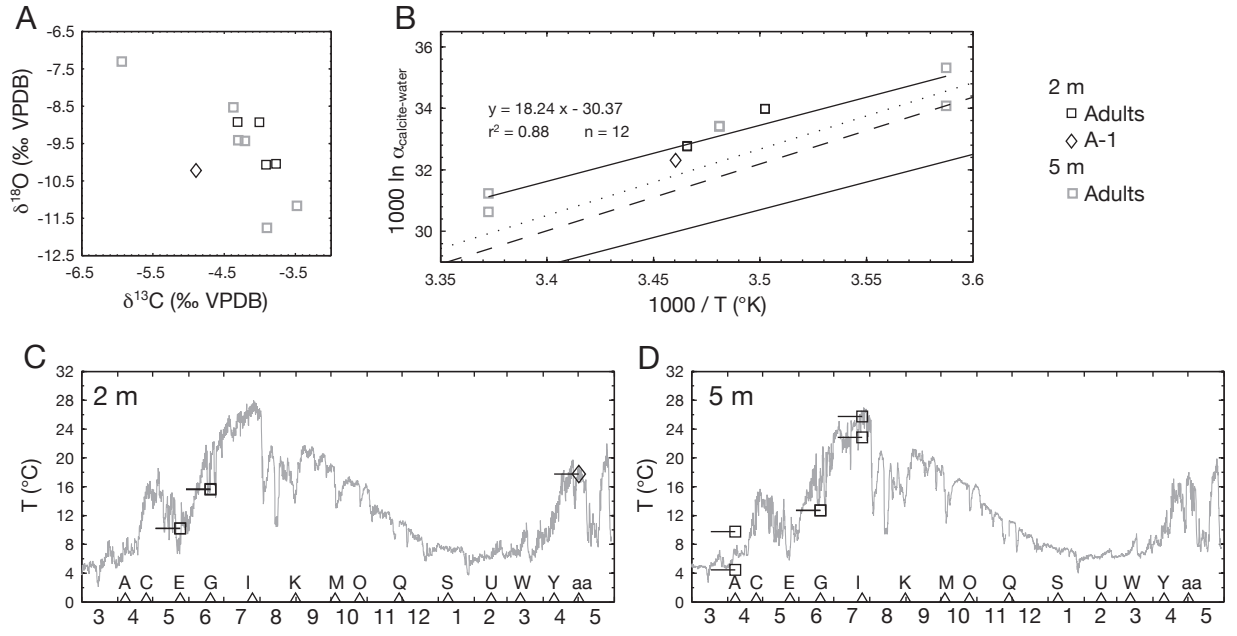

FIGURE AI.*Pz*.1
Oxygen isotope compositions of *Prionocypris zenkeri* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures at 2 m water depth (C); same as for C but at 5 m water depth (D).

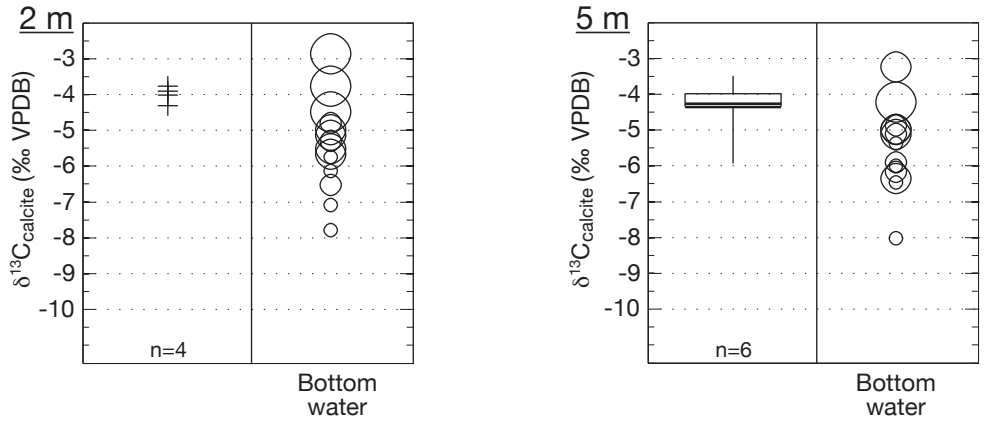

FIGURE AI.*Pz*.2
Carbon isotope compositions of *Prionocypris zenkeri* valves and values for a calcite grown in equilibrium with DIC of bottom water DIC at 2 and 5 m water depths.

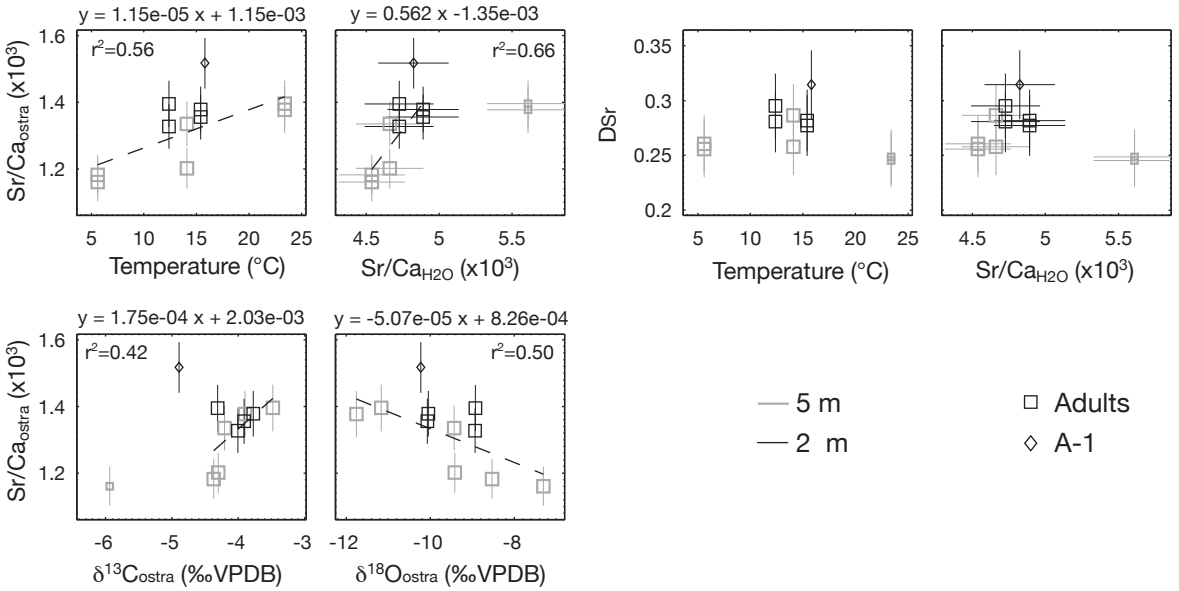

FIGURE AI.*Pz*.3
Sr/Ca and D_{Sr} of *Prionocypris zenkeri* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Herpetocypris reptans

(Baird, 1835)

Herpetocypris reptans has been collected from 2 to 13 m depth. Qualitative observations suggest that the population at 5 m is slightly more important than at 2 m depths. At these two sites, the species belongs to the four most dominant species. At 13 m, the total population density (A-7 to adult) is 1000 Ind/m^2. If only stages A-4 to adult are considered, the density is 700 Ind/m^2, representing 3.6 % of the entire population (Fig. 3.7). In terms of number of individuals, the population is indeed not very important, but taking the considerable size of the specimens of this species into account, *H. reptans* is much more significant in terms of biomass and resource needs.

Development at 2 and 5 m is difficult to assess because of the scarce, scattered and sporadic recovery of specimens plus the long life span of the adults. However, at 13 m, it is possible to identify a first generation hatching in spring and reaching maturity in September. Abundance of juveniles in late autumn and winter as well as presence of adults throughout the year suggests that the species also produces a winter generation at this depth (Fig 3.9). Presence of two generations at 13 m is confirmed by the oxygen isotope compositions for adult and juvenile valves. In the two shallower sites, the oxygen isotope composition of the adults reflects only warm temperatures indicating

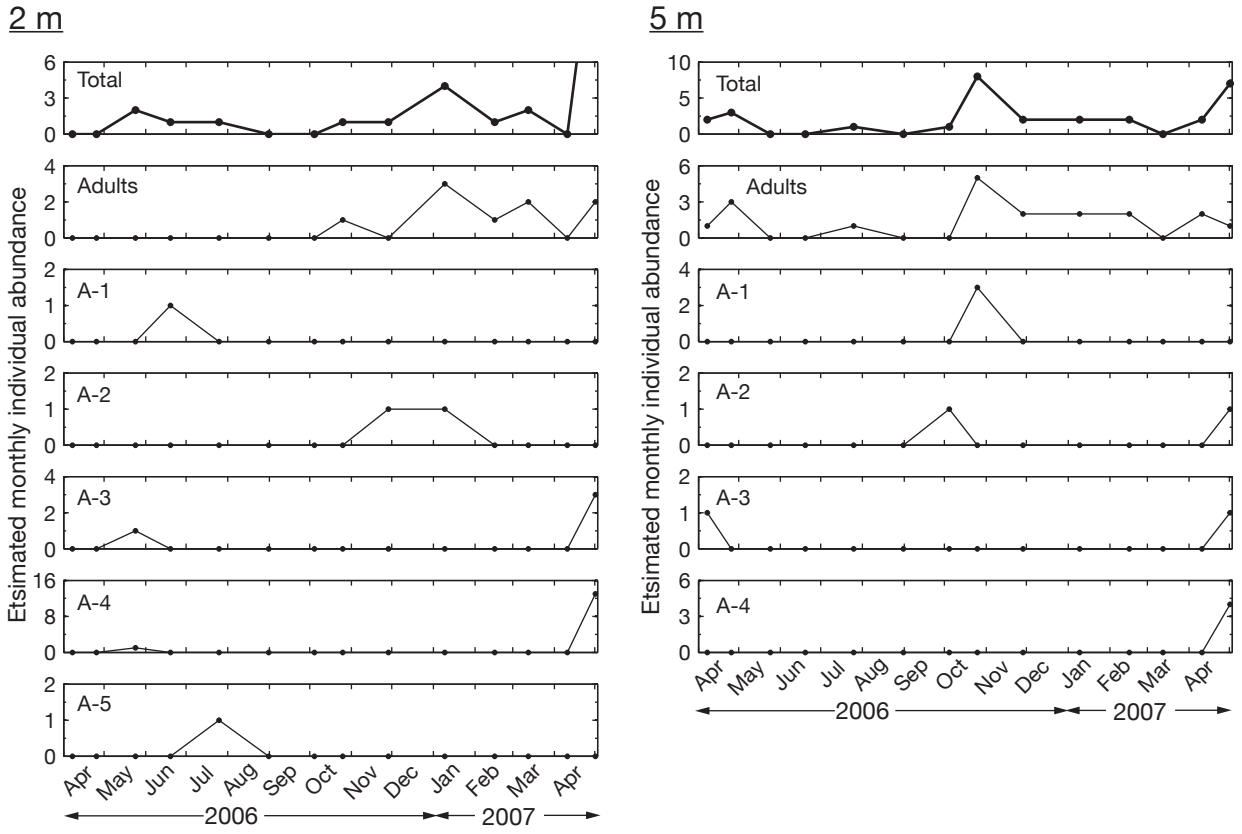

FIGURE AI.*Hr*.1a
Estimated monthly individual abundances of *Herpetocypris reptans* at 2 and 5 m water depths.

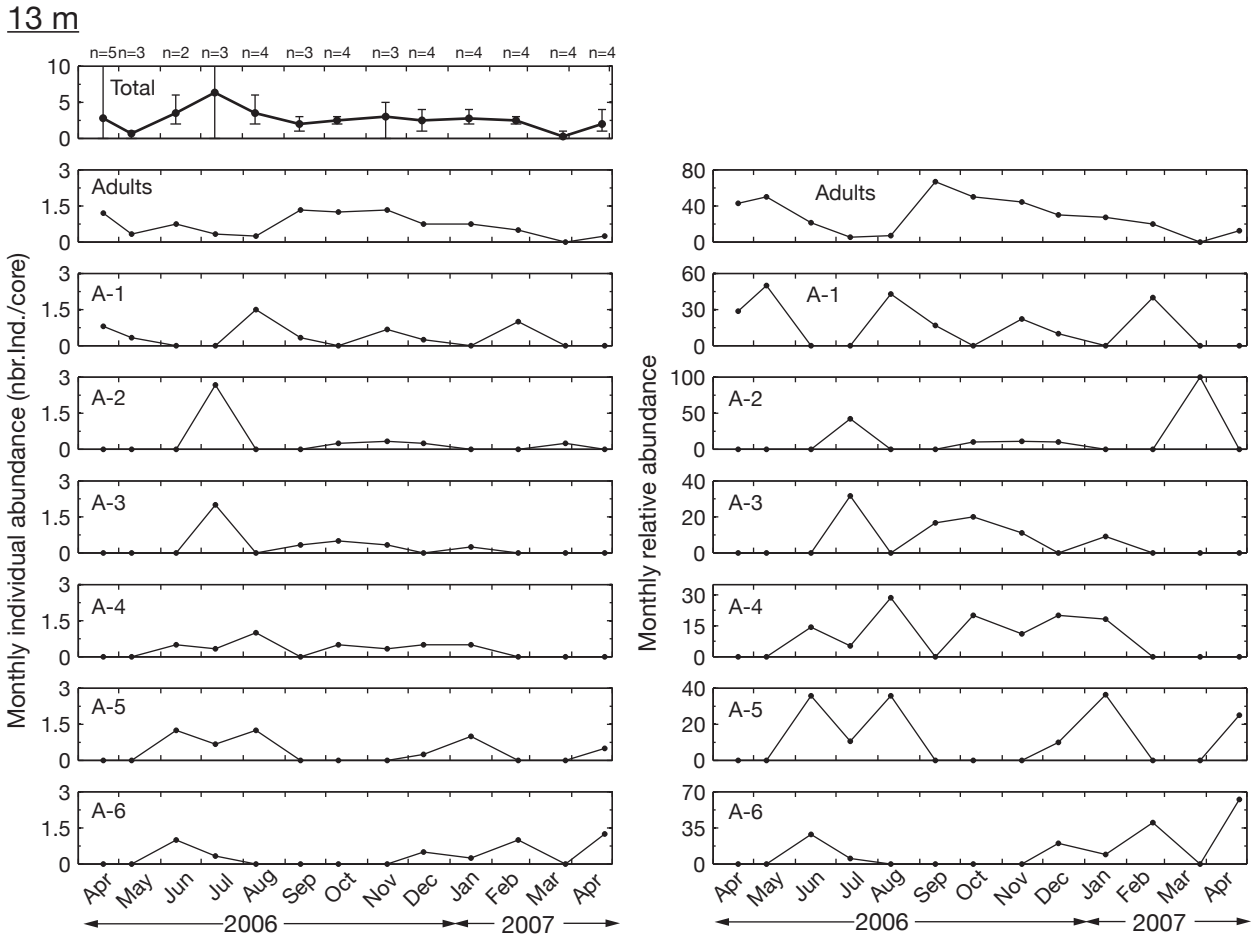

FIGURE AI.*Hr*.1b
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Herpetocypris reptans* at 13 m water depth.

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that, in the littoral zone, adults moult during warm months, i.e. from May to October.

At 2 m depth, the animals were recovered from pebbles and algae, at 5 m, from sand and algae. At 13 m depth, *H. reptans* was found surprisingly deep within the sediment. Younger juveniles are mostly found in the top half-centimetre, older juveniles down to 1.5 cm. The majority of the adults were collected between 0.5 and 1.5 cm, few were found in the first centimetre, and, individuals were occasionally found down to 3 cm (Fig. 3.10).

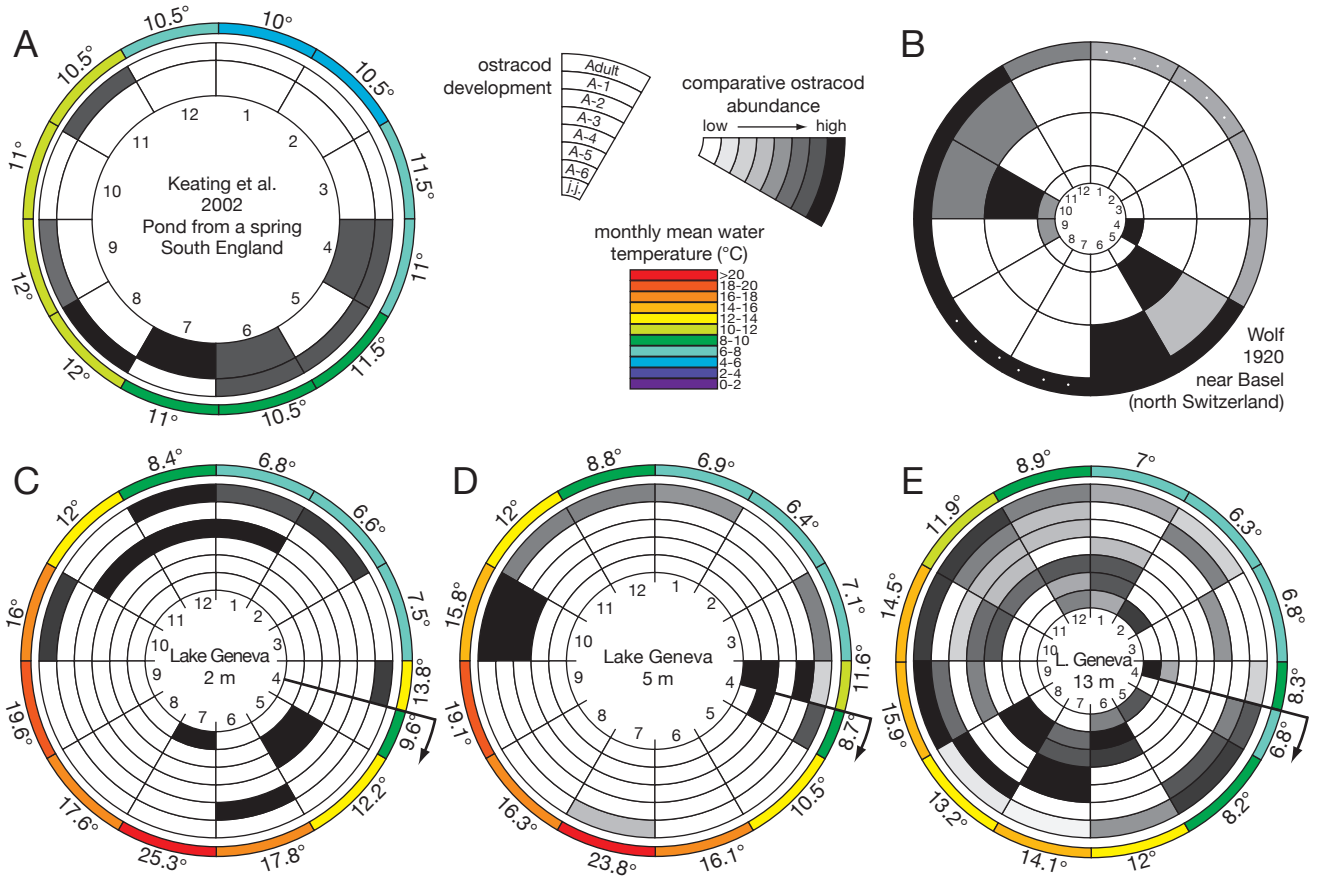

FIGURE AI.*Hr*.2
Life-cycles of *Herpetocypris reptans* in different localities illustrated with SOWM. Data from: Keatings et al., 2002 (A); Wolf, 1920 (B); and present study (C, D, and E).

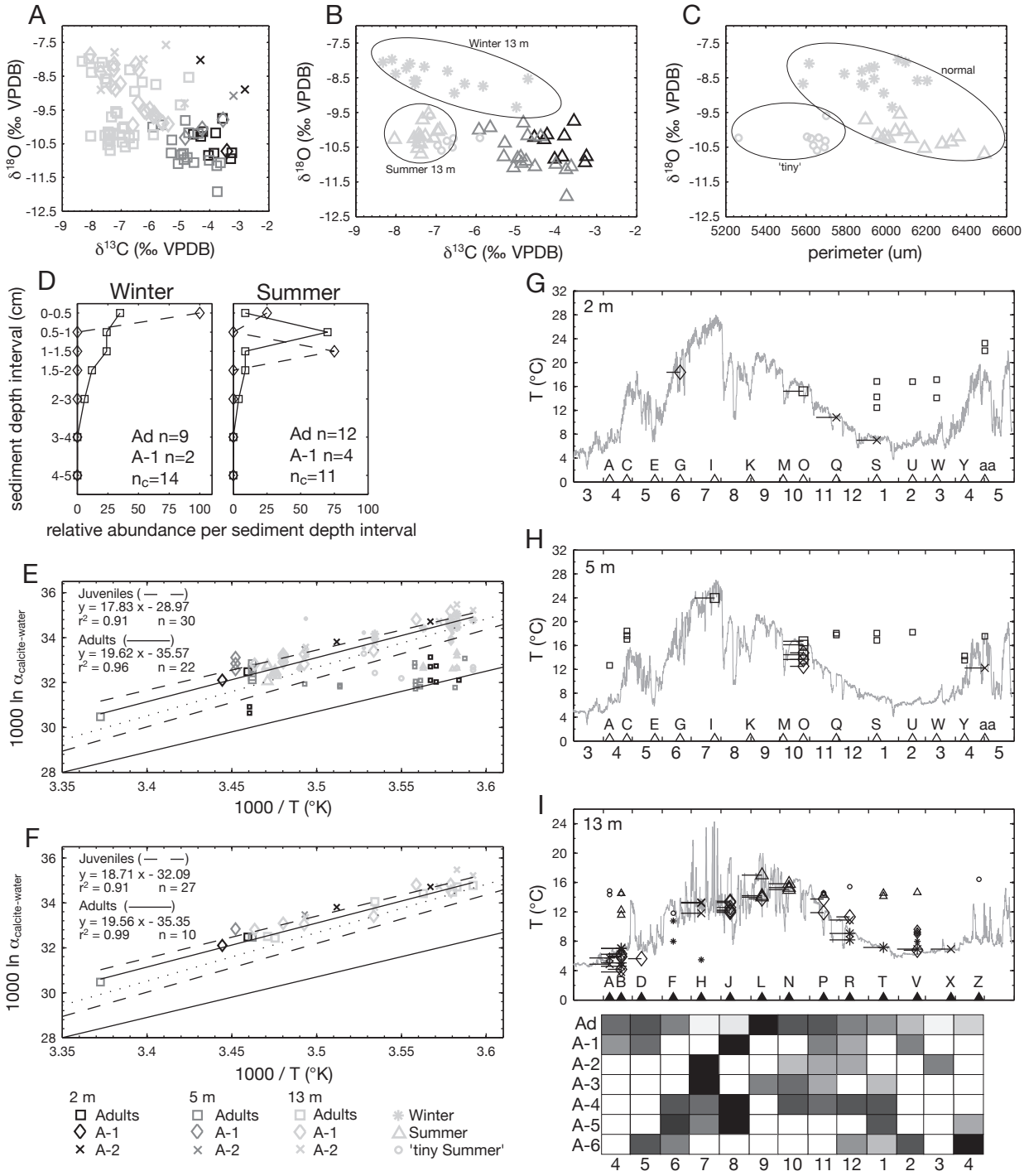

FIGURE AI.*Hr*.3

Oxygen isotope compositions of *Herpetocypris reptans* valves: oxygen versus carbon isotope compositions (A); same as A but only for adults (B); adult oxygen isotope compositions versus valve perimeters (C); winter and summer sediment penetration depths of adults and A-1 juveniles (D); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (E); same as E but using monthly averages (F); water temperature and $\delta^{18}O$ recalculated calcification temperatures at 2 m water depth (G); same as for G but at 5 m water depth (H); same as G but at 13 m water depth with illustration of the species life-cycle at this depth (I).

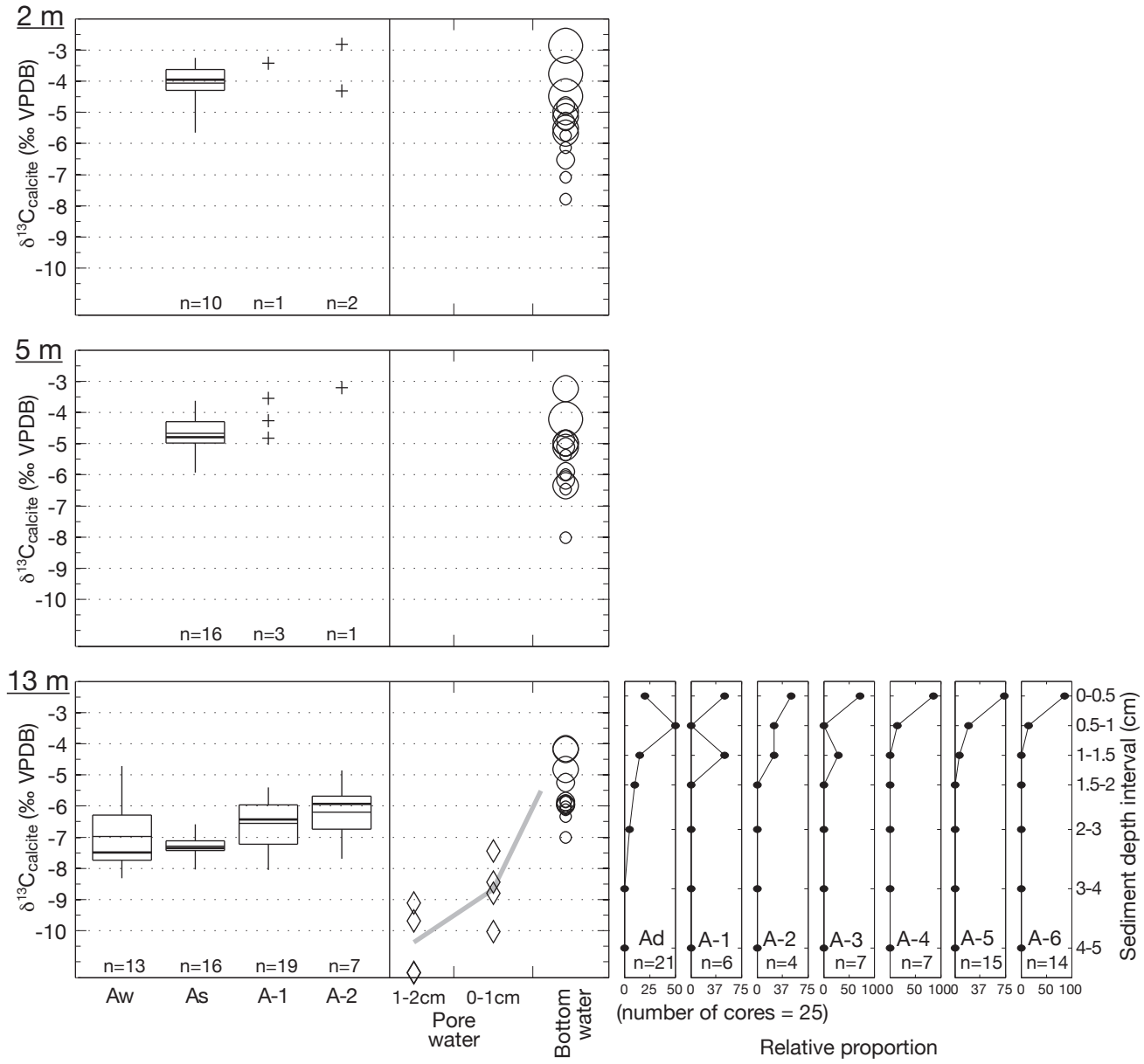

FIGURE AI.*Hr*.4
On the left side: carbon isotope compositions of *Herpetocypris reptans* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water DIC at 2, 5 and 13 m water depths. On the right side: observed sediment penetration depths of *Herpetocypris reptans* at 13 m water depths.

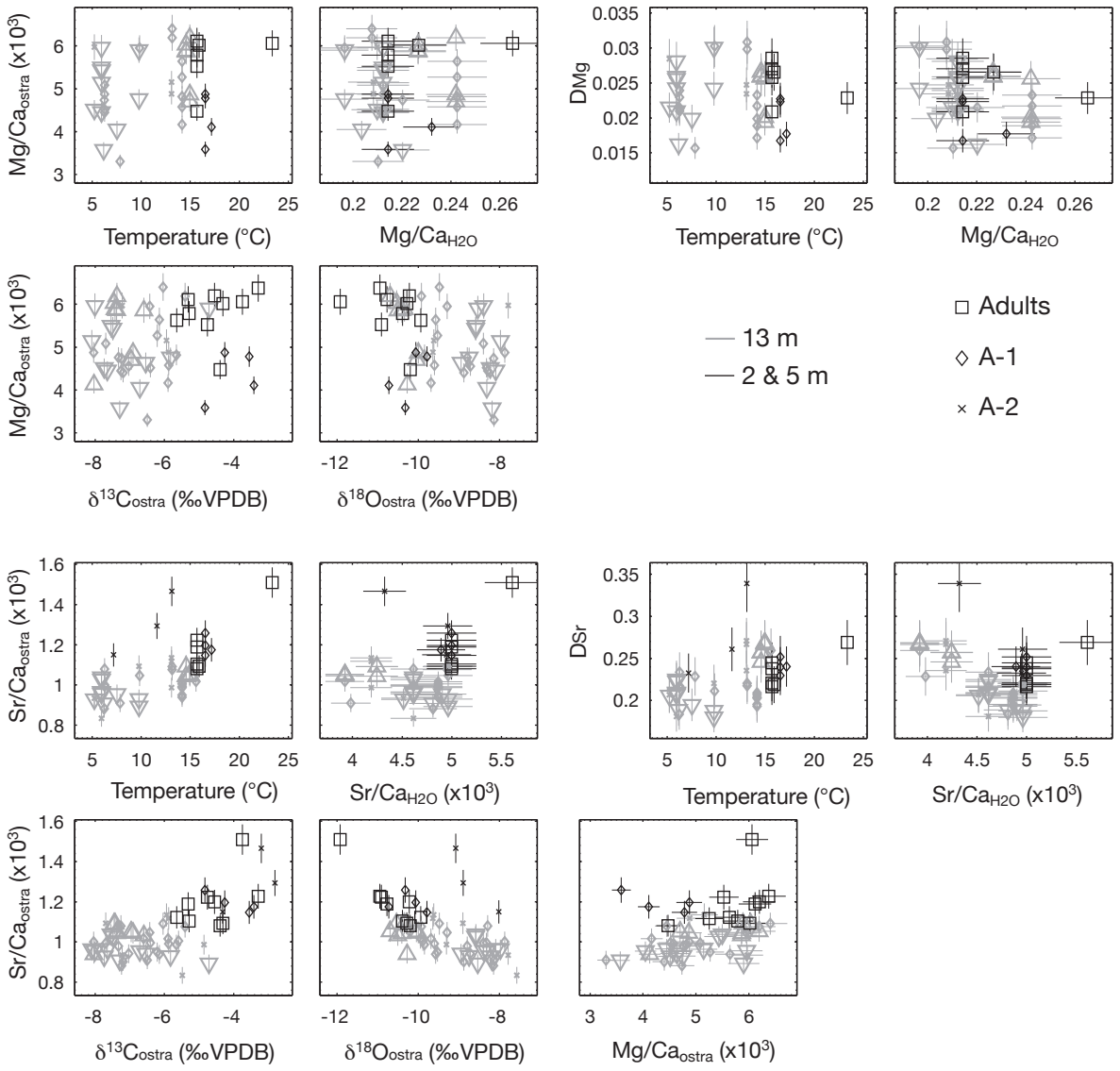

FIGURE AI.*Hr*.5
Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr} of *Herpetocypris reptans* valves versus water temperature, Mg/Ca or Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Isocypris beauchampi

(Paris, 1920)

Isocypris beauchampi is very rare in Lake Geneva and occurs mainly in the sublittoral zone. Population density (A-4 to Ad) is 75 and 26 Ind/m^2 at 13 and 33 m depths, respectively, representing only 0.3 and 0.4 % of the entire population at the respective depths (Fig. 3.7). Their rare occurrence in space and time make it difficult to establish the development of the species. Juveniles were found throughout the year, adults in spring, summer and winter. Specimens of *I. beauchampi* were usually found in the top half-centimetre of the sediment.

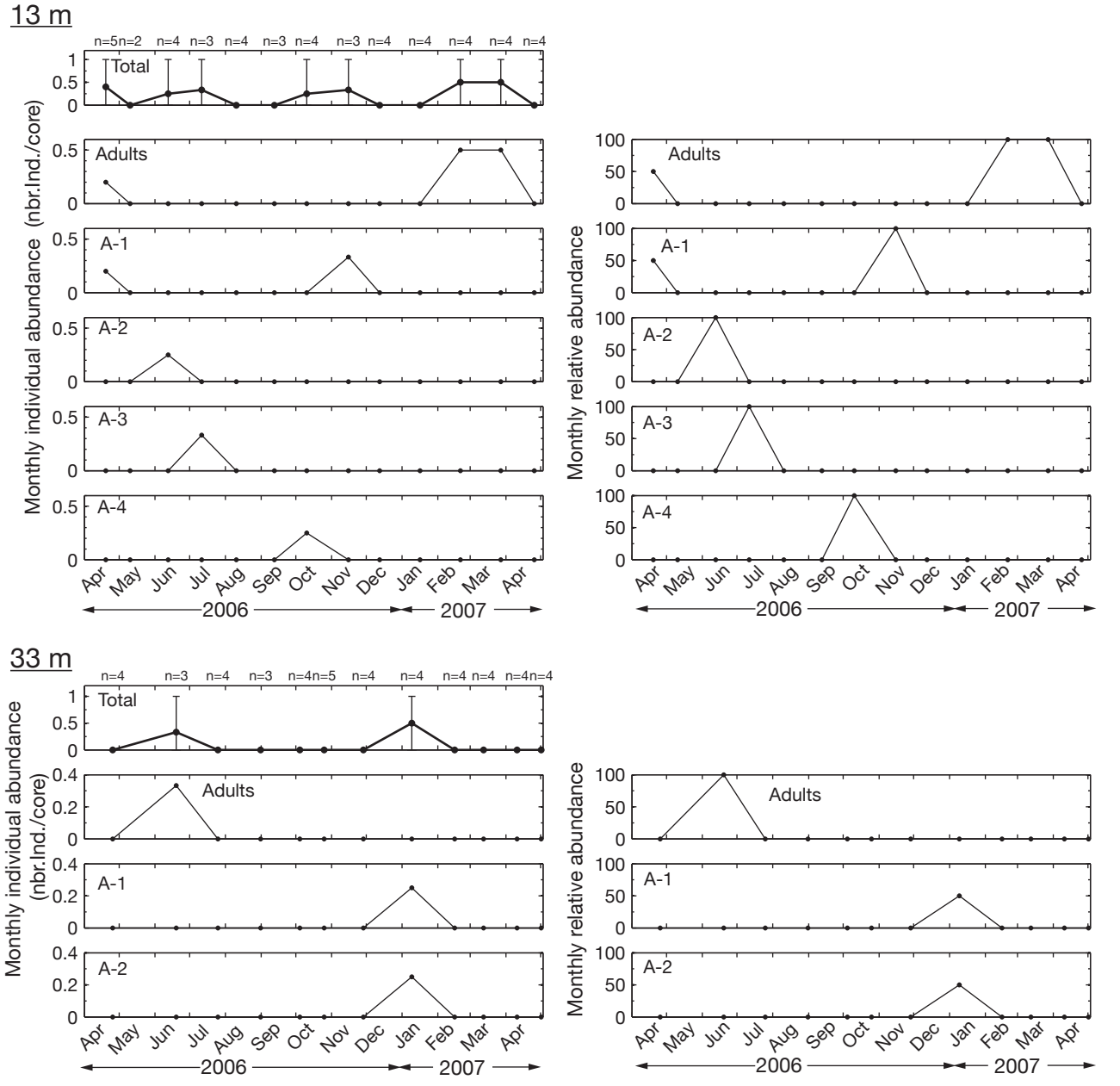

FIGURE AI.*Ib*.1
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Isocypris beauchampi* at 13 and 33 m water depths.

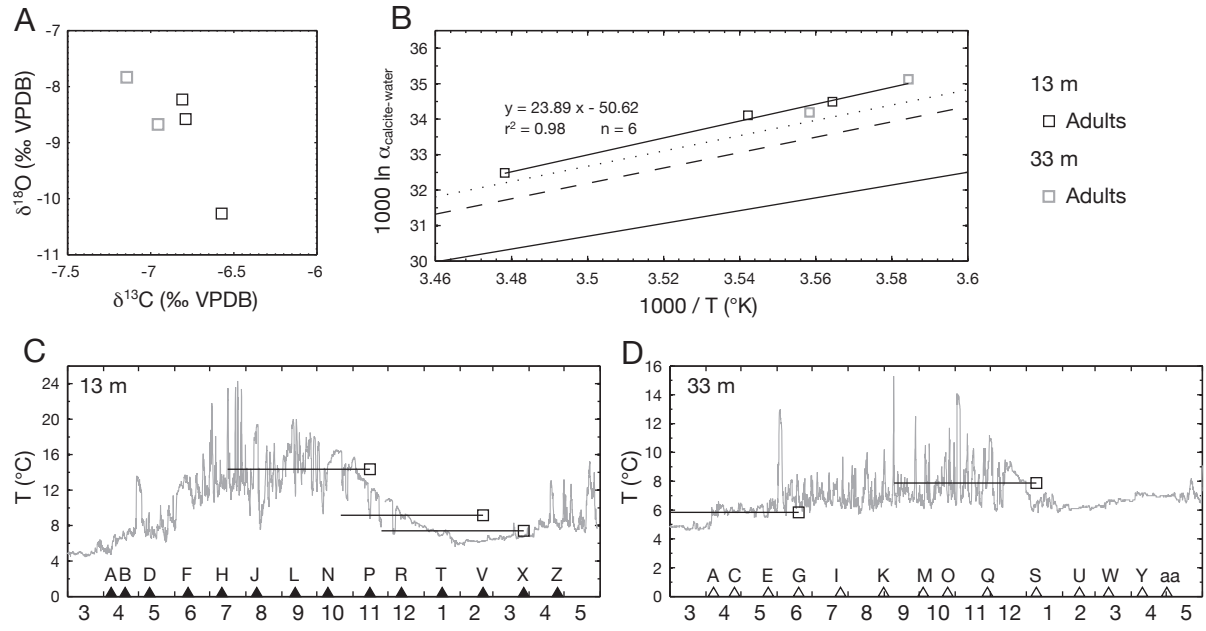

FIGURE AI.*Ib*.2
Oxygen isotope compositions of *Isocypris beauchampi* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures at 13 m water depth (C); same as for C but at 33 m water depth (D).

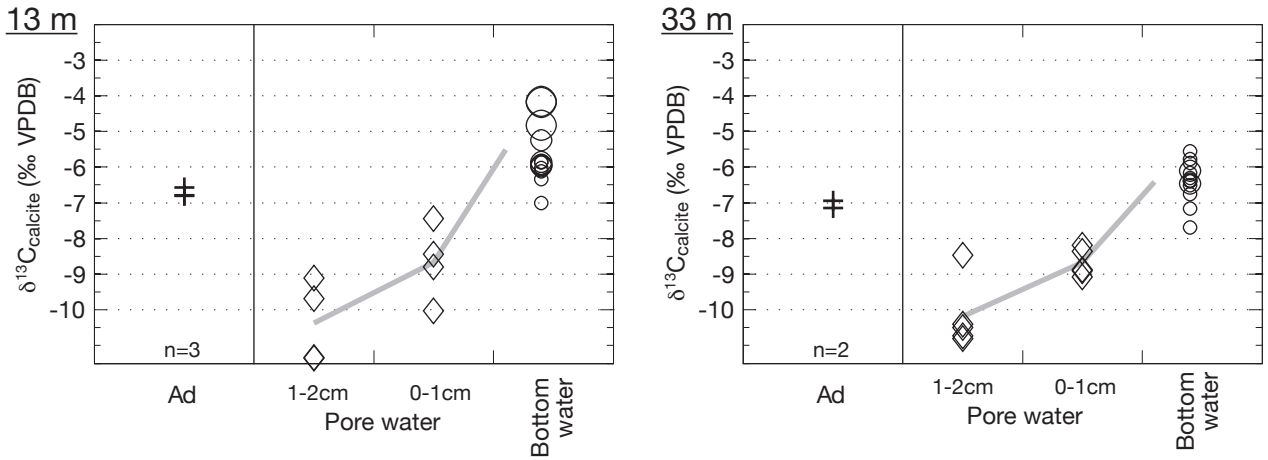

FIGURE AI.*Ib*.3
Carbon isotope compositions of *Isocypris beauchampi* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 13 and 33 m water depths.

Cypridopsis vidua

(O.F. Müller, 1776)

Cypridopsis vidua is a typical littoral species that is very abundant at 2 m, and slightly less abundant at 5 m. Relative comparison ranks *C. vidua* as the dominant species at 2 m and second in terms of abundance at 5 m depth. Very rare living specimens can be reworked down to larger depths of the basin (Fig. 3.7).

Higher population density of *C. vidua* was found from July to October. The geochemical analyses of the valve also suggest that two generations develop during the year, the first reaches maturity in June and July, the second in September and October. The cold winter 2005-2006 resulted in the death of all specimens of *C. vidua*, which is why none were found in April 2006. The winter 2006-2007 was, in contrast, especially mild and specimens of *C. vidua* were sampled almost throughout the winter (Fig. 3.9). Oxygen isotope compositions of adult valves indicate that moulting occurred at water temperatures of at least 17 °C (*Chapter V-1*).

C. vidua was mainly found on pebbles and in algae at 2 m and in sand and algae at 5 m depth.

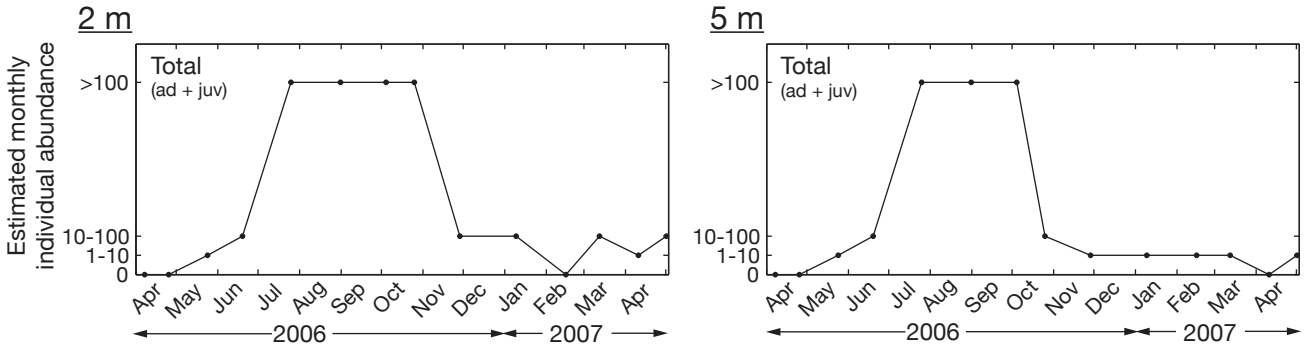

FIGURE AI.*Cv*.1
Estimated monthly individual abundances of *Cypridopsis vidua* at 2 and 5 m water depths.

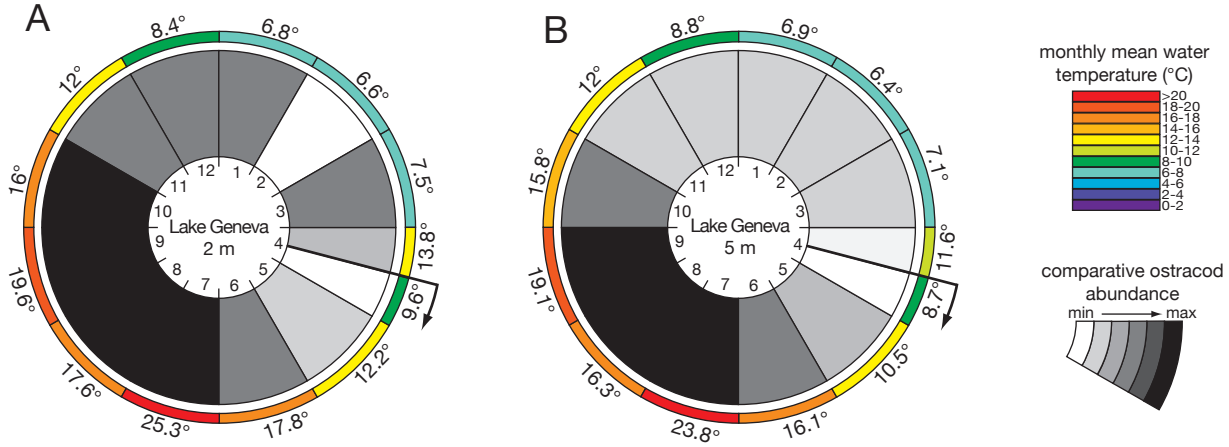

FIGURE AI.*Cv*.2
Life-cycles of *Cypridopsis vidua* illustrated with SOWM at 2 and 5 m water depths.

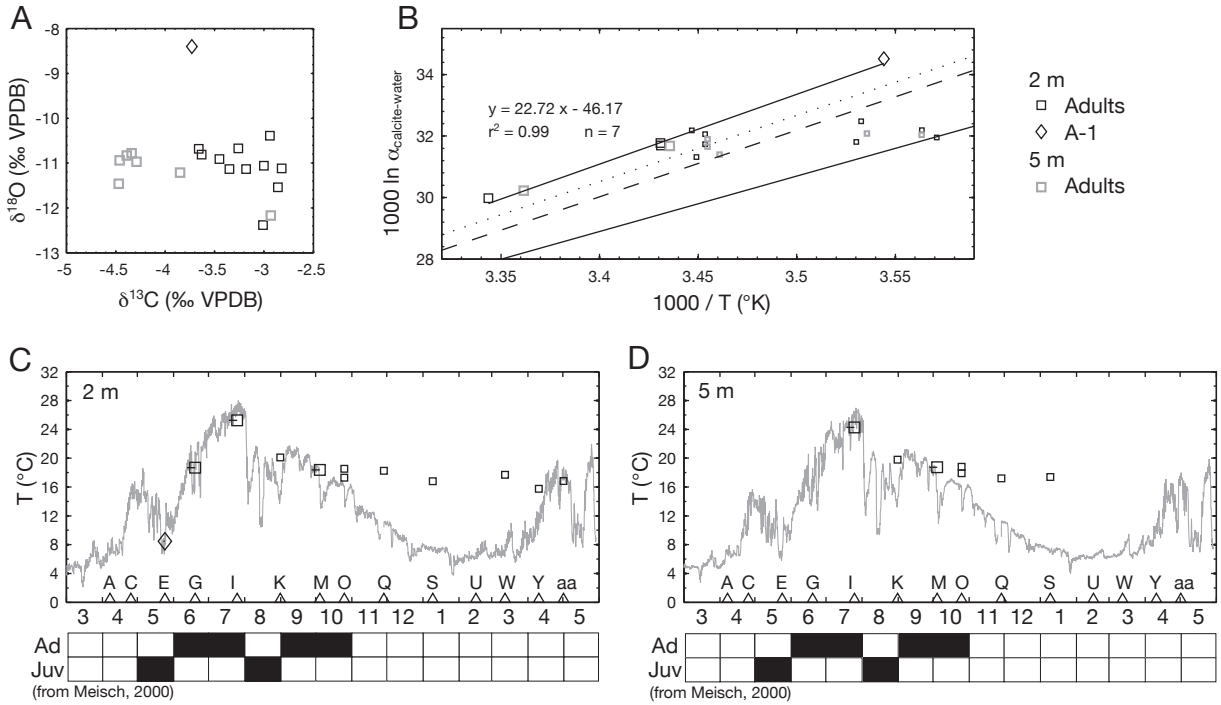

FIGURE AI.*Cv*.3
Oxygen isotope compositions of *Cypridopsis vidua* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle (Meisch, 2000) at 2 m water depth (C); same as for C but at 5 m water depth (D).

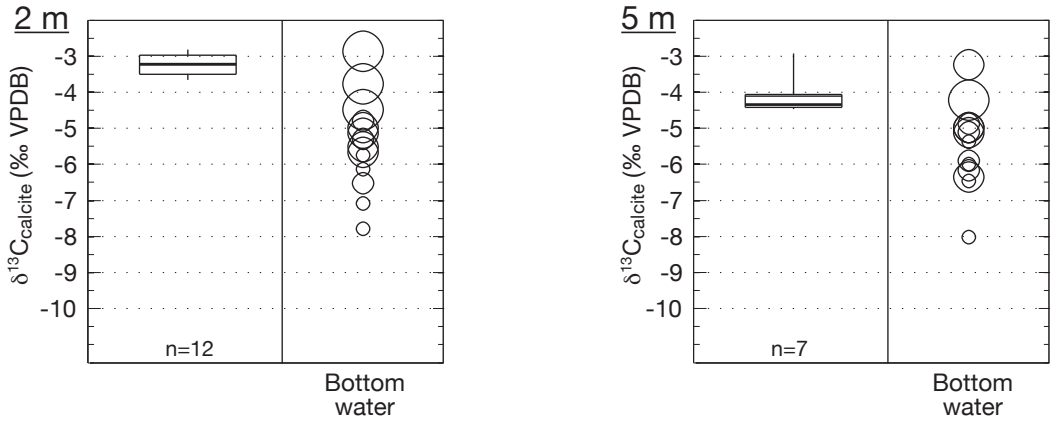

FIGURE AI.*Cv*.4
Carbon isotope compositions of *Cypridopsis vidua* valves and values for a calcite grown in equilibrium with DIC of bottom water at 2 and 5 m water depths.

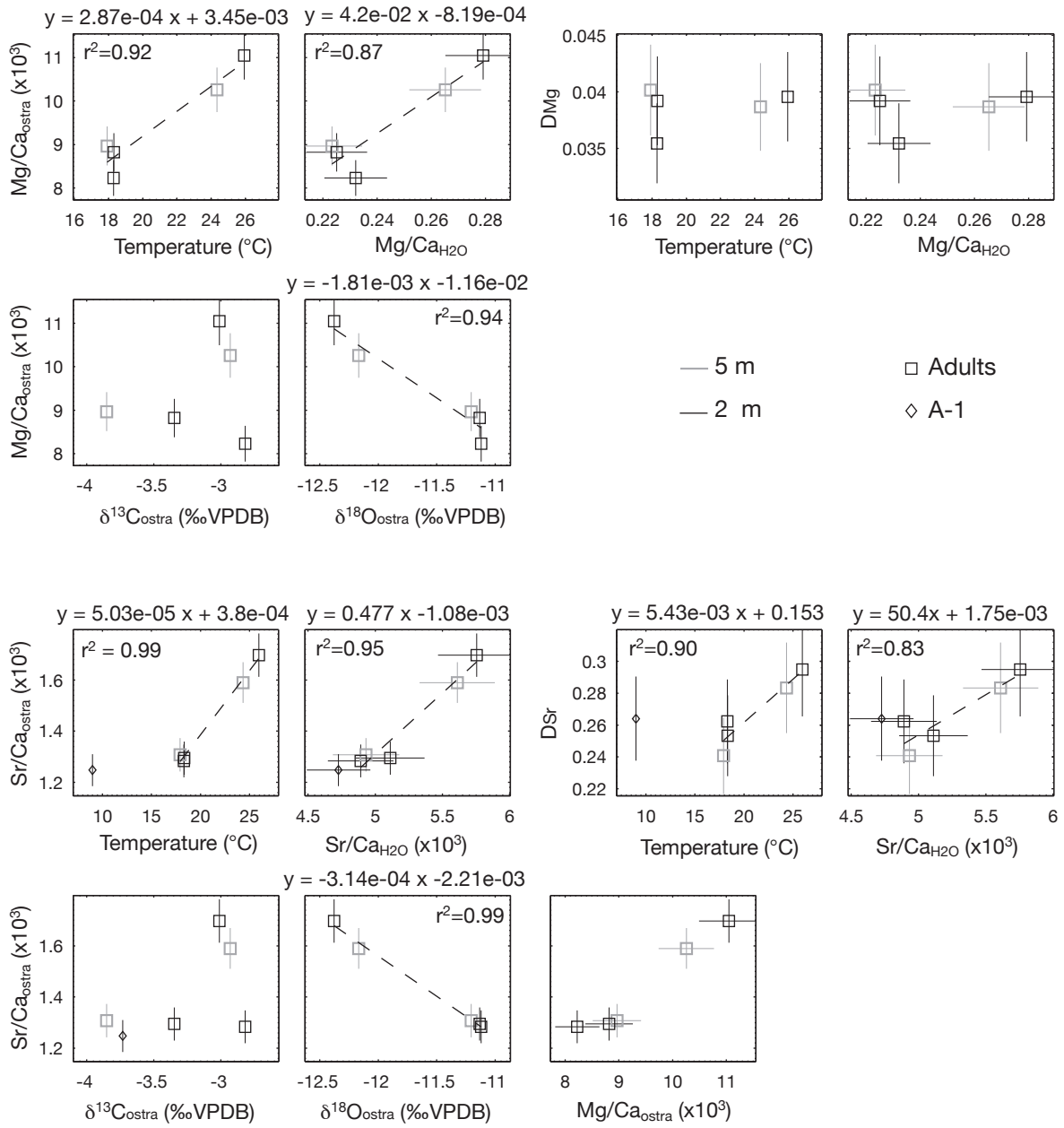

FIGURE AI.*Cv*.5
Mg/Ca, D_{Mg}, Sr/Ca, and D_{Sr} of *Cypridopsis vidua* valves versus water temperature, Mg/Ca and Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Plesiocypridopsis & Potamocypris

Pleisocypridopsis newtoni (Brady & Robertson, 1870)

Potamocypris similis G. W. Müller, 1912

Potamocypris smaragdina (Vávra, 1891)

Plesiocypridopsis newtoni is very rare, and was sampled only at one occasion at 2 m depth in July (Fig. 3.7). Rare specimens were collected during summer in other shallow littoral zones, suggesting that the species could be more abundant in other sites.

Potamocypris similis is rare in Lake Geneva. Juveniles and adults were only recovered on pebbles at 2 m depths in June, some adults were sampled in July and only 1 adult in January (Fig. 3.7).

Potamocypris smaragdina is rare in Lake Geneva. The majority of the specimens were recovered on pebbles at 2 m depths in June and July. Two specimens were sampled in July at 5 m depth in sand (Fig. 3.7).

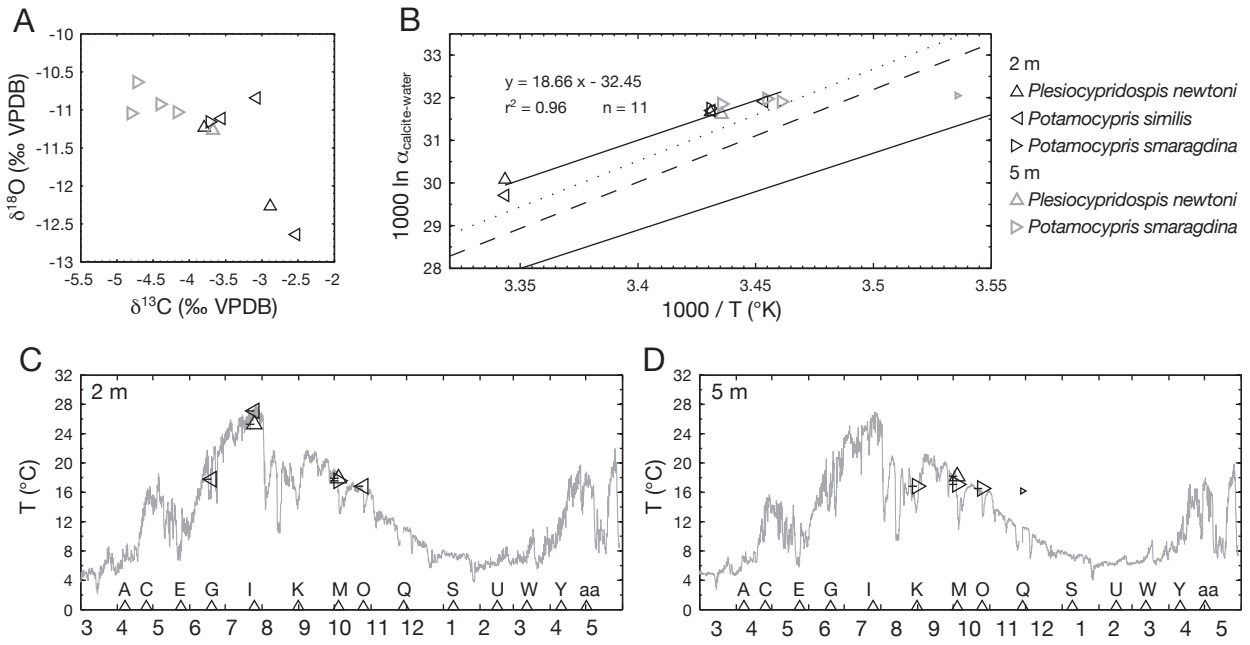

FIGURE AI.*PP*.1
Oxygen isotope compositions of *Plesiocypridopsis newtoni*, *Potamocypris similis*, and *Potamocypris smaragdina* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures at 2 m water depth (C); same as for C but at 5 m water depth (D).

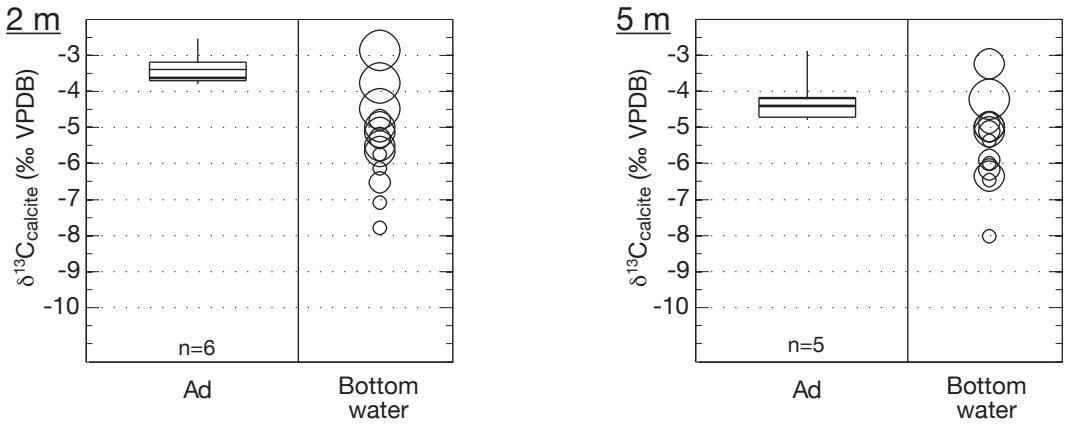

FIGURE AI.*PP*.2
Carbon isotope compositions of *Plesiocypridopsis newtoni*, *Potamocypris similis*, and *Potamocypris smaragdina* valves and values for a calcite grown in equilibrium with DIC of bottom water DIC at 2 and 5 m water depths.

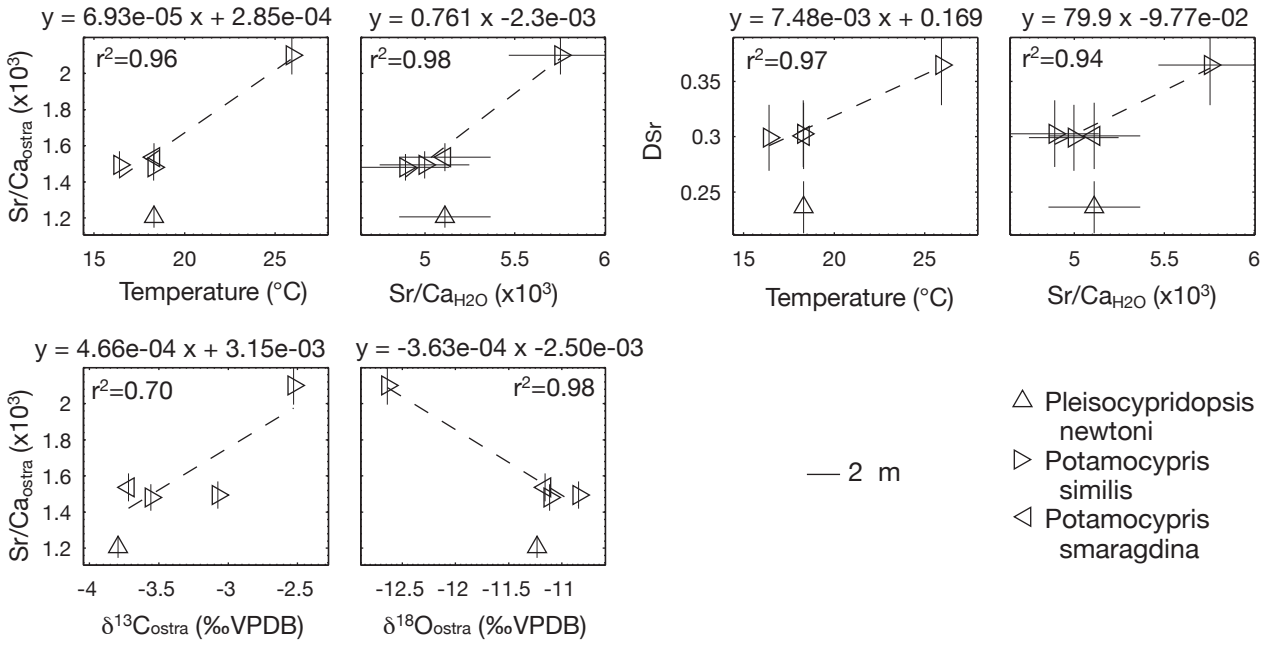

FIGURE AI.*PP*.3
Sr/Ca and D_{Sr} of *Plesiocypridopsis newtoni*, *Potamocypris similis*, and *Potamocypris smaragdina* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Limnocythere inopinata

(Baird, 1843)

Limnocythere inopinata was recovered from 2 to 13 m depths. The very rare living specimens found at 33 m have been reworked from shallower sites. Qualitative observations suggest that its abundance peaks at 5 m depth, where the species is the third most important. At 13 m depths, population density is estimated at 400 Ind/m^2, representing 2.1 % of the entire population (Fig. 3.7).

No specimens were found in April following the cold winter 2005-2006, but as water temperature rises in May, the quantity of adults and juveniles increases rapidly at 2 and 5 m depth. The first occurrence at 13 m is delayed by one month relative to the shallower sampling sites and higher abundance is only reached in July and August. The specimens disappear gradually as temperature decreases in autumn and very few specimens were recovered during the exceptionally mild winter 2007 (Fig. 3.9).

L. inopinata prefers to live on pebbles at 2 m and in the sand at 5 m. At 13 m, most of the specimens of *L. inopinata* were sampled near to the surface; 2/3 of the specimens were found in the top half-centimetre, the rest of the population in the following half-centimetre of sediment, but the number of samples remains small, making it difficult to verify these first observations.

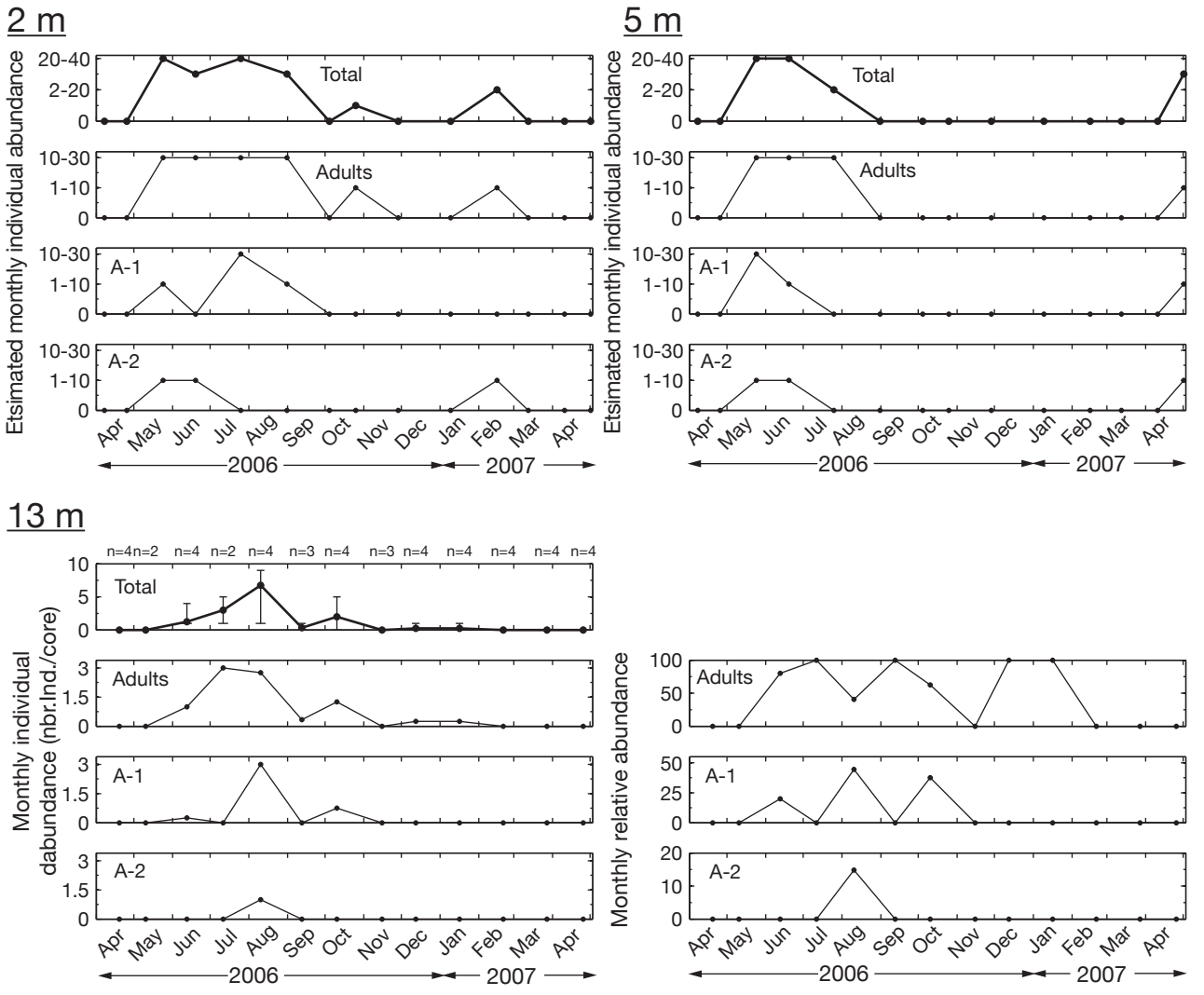

FIGURE AI.*Li*.1
Estimated monthly individual abundances at 2 and 5 m water depth and monthly individual abundances and monthly relative abundances of *Limnocythere inopinata* at 13 m water depth.

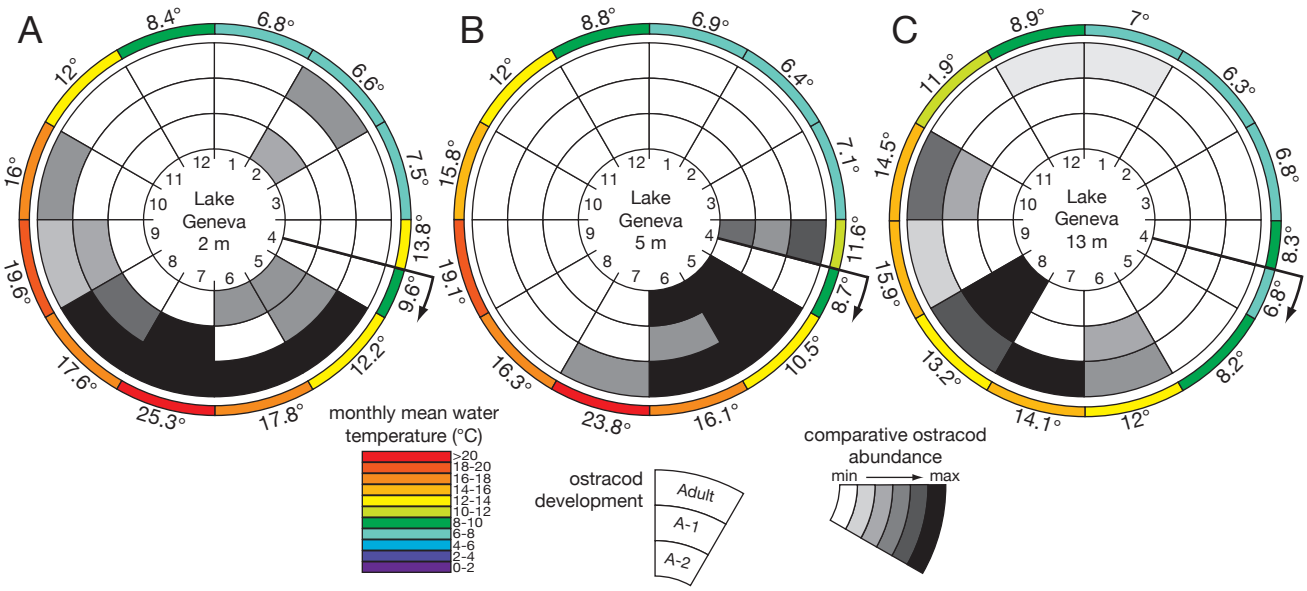

FIGURE AI.*Li*.2
Life-cycles of *Limnocythere inopinata* illustrated with SOWM at 2, 5 and 13 m water depths.

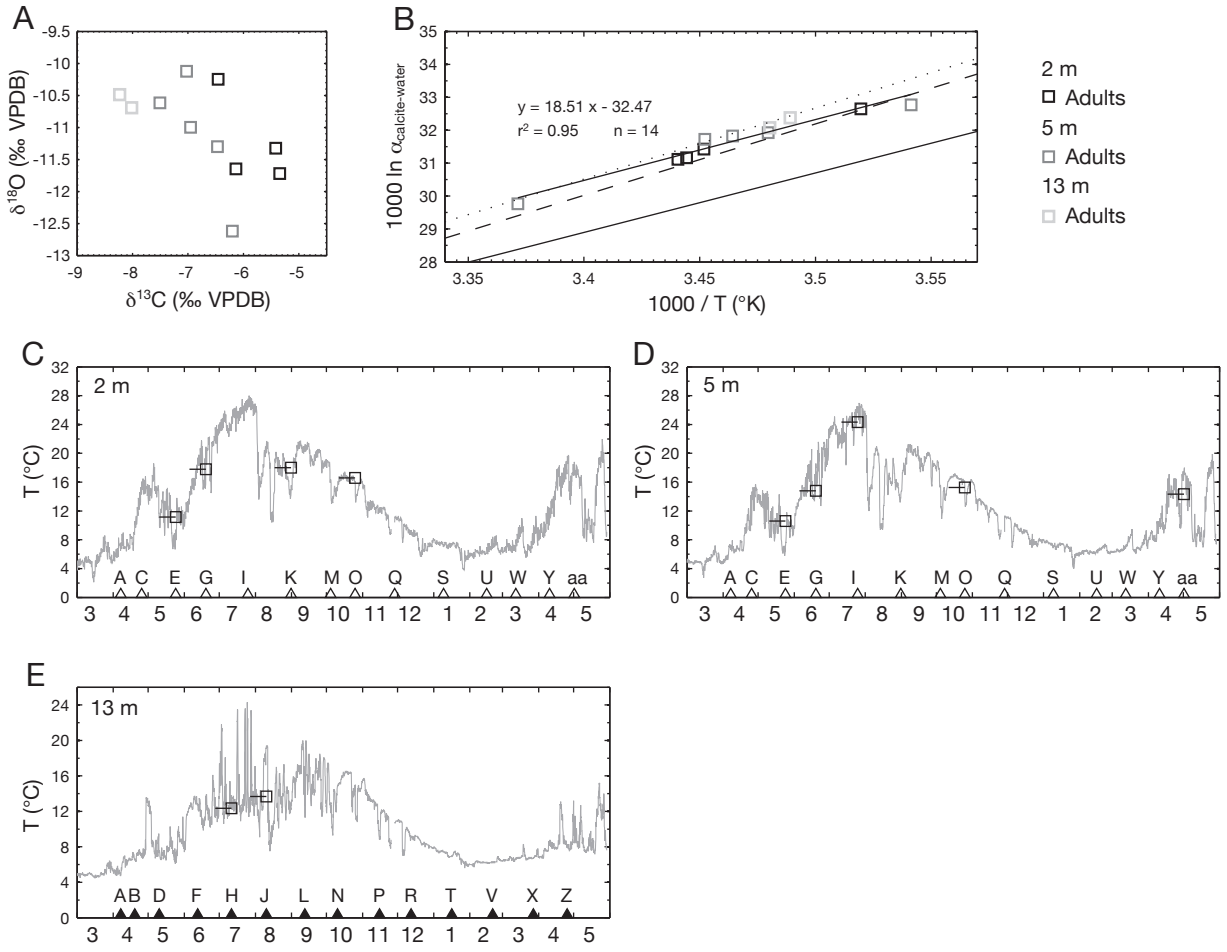

FIGURE AI.*Li*.3
Oxygen isotope compositions of *Limnocythere inopinata* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ re-calculated calcification temperatures at 2 m water depth (C); same as for C but at 5 m water depth (D); same as C but at 13 m water depth (E).

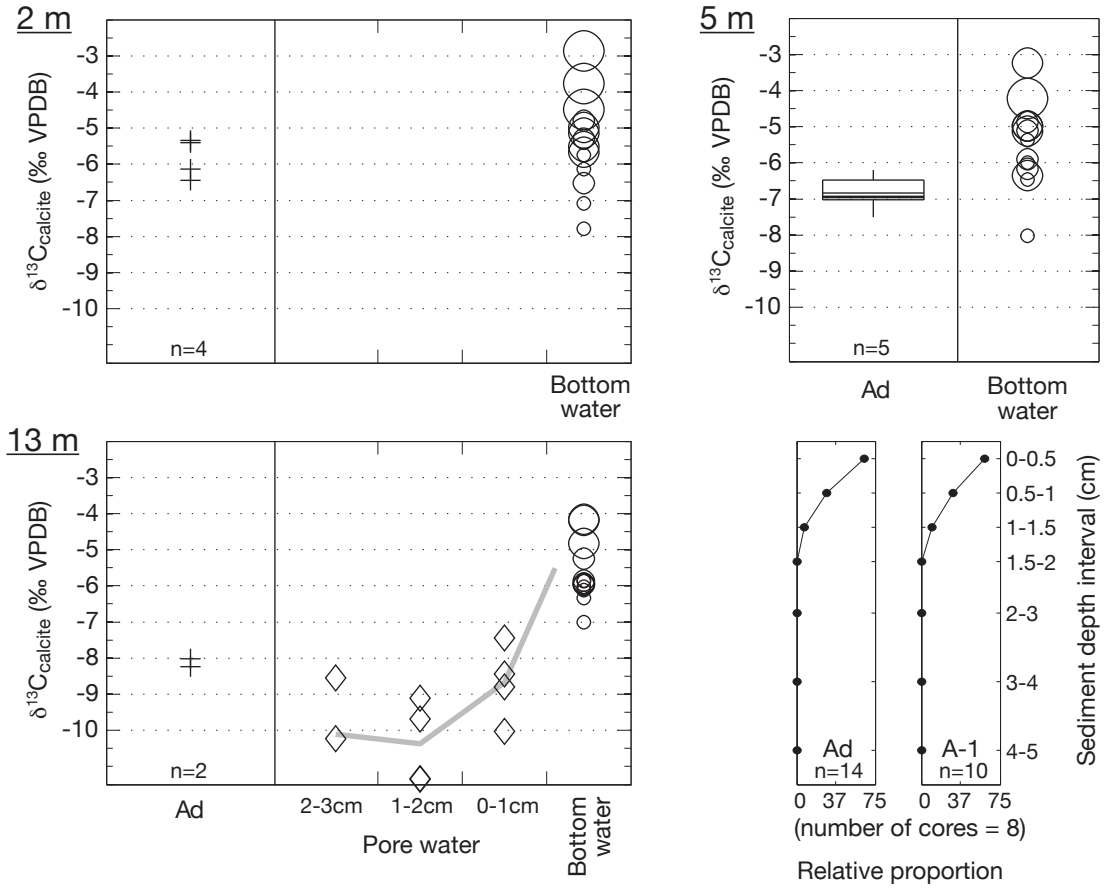

FIGURE AI.*Li*.4
Carbon isotope compositions of *Limnocythere inopinata* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 2, 5 and 13 m water depths. Sediment penetration depths of *Limnocythere inopinata* at 13 m water depth is illustrated on the right side of the figure.

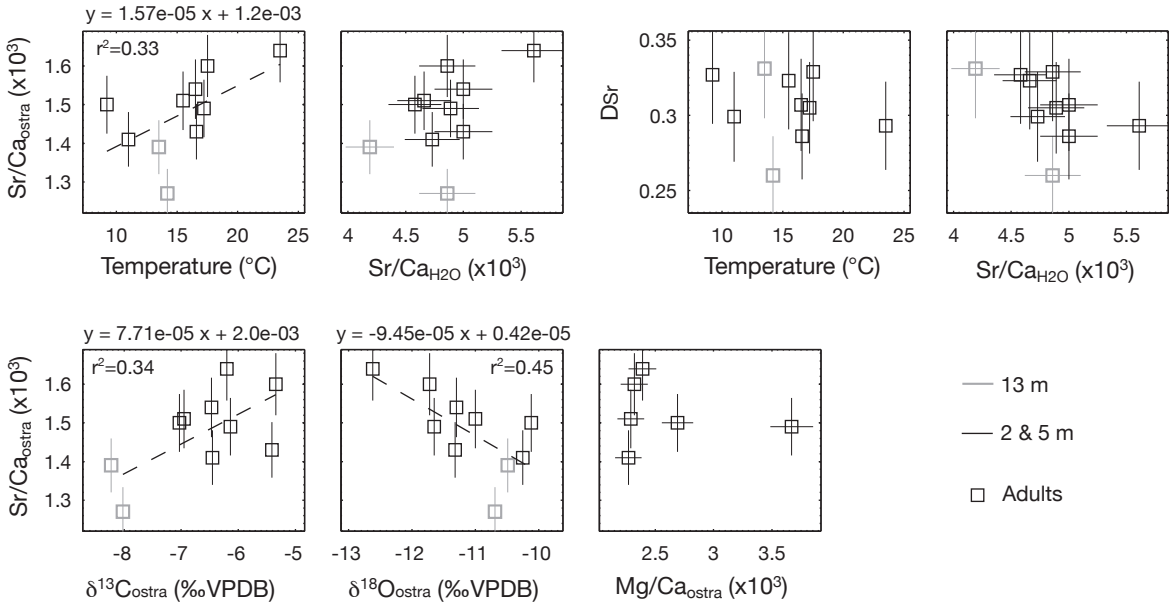

FIGURE AI.*Li*.5
Sr/Ca and D_{Sr} of *Limnocythere inopinata* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Limnocytherina sanctipatricii

(Brady & Robertson, 1869)

Limnocytherina sanctipatricii was only found at 13 m depth. Its abundance is quite low and only 530 Ind/m² were collected, representing 2.8 % of the entire population (Fig. 3.7).

Specimens of *L. sanctipatricii* were sampled from December to July. The presence of different juvenile stages in early winter suggests that *L. sanctipatricii* develops rapidly. First adults are found in February and females survive until July, males vanishing generally earlier. Patterns of juvenile and adult abundances on the SOWM suggest that the development occurs by pulses. It is not clear if the species generates one population per year that grow by pulses timed by favourable environmental factors or if two or more generations are produced. Population abundance in early spring 2006 is twice to three times higher than that in early spring 2007, suggesting that the relatively warm water temperature during winter 2006-2007 prevented the development of *L. sanctipatricii* (Fig. 3.9).

L. sanctipatricii does not dig actively in the sediment (Fig. 3.10). 2/3 to 3/4 of the specimens, depending of the development stage, are found in the top half-centimetre. The rest of the population is found in the centimetre underneath.

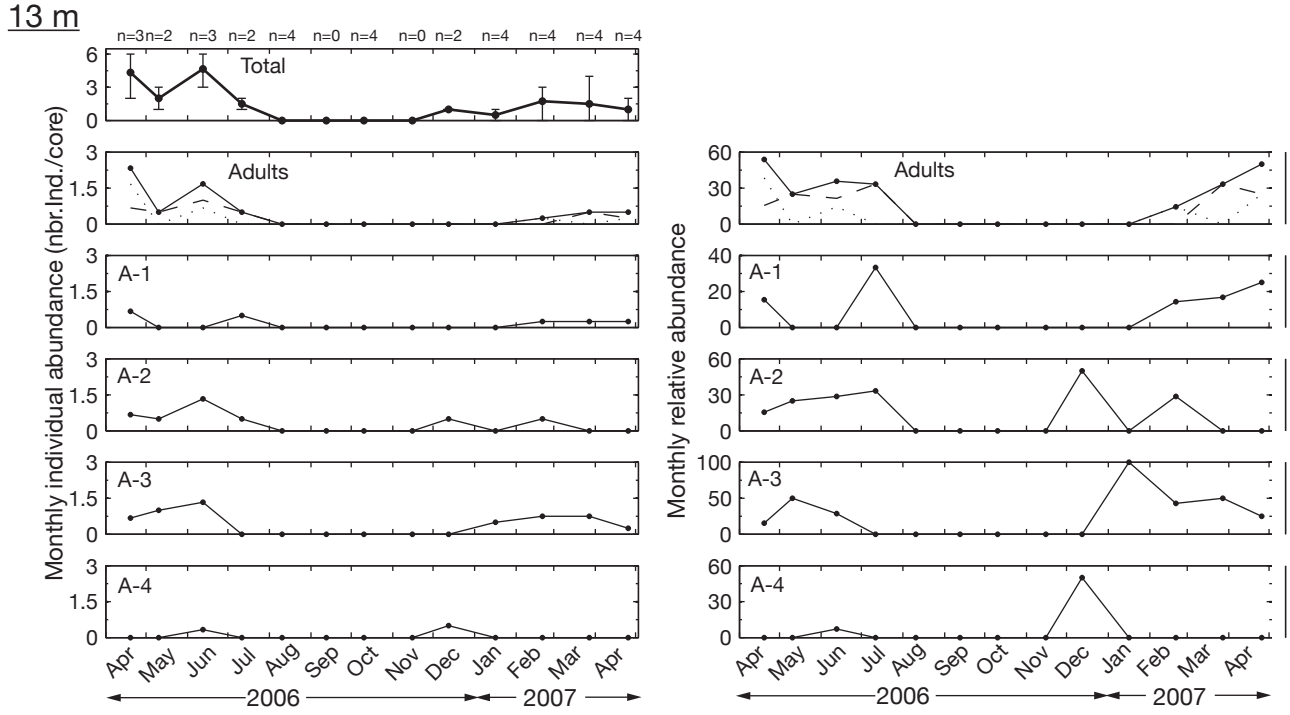

FIGURE AI.*Ls*.1
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Limnocytherina sanctipatricii* at 13 m water depth. Dashed lines stand for females, dotted lines for males.

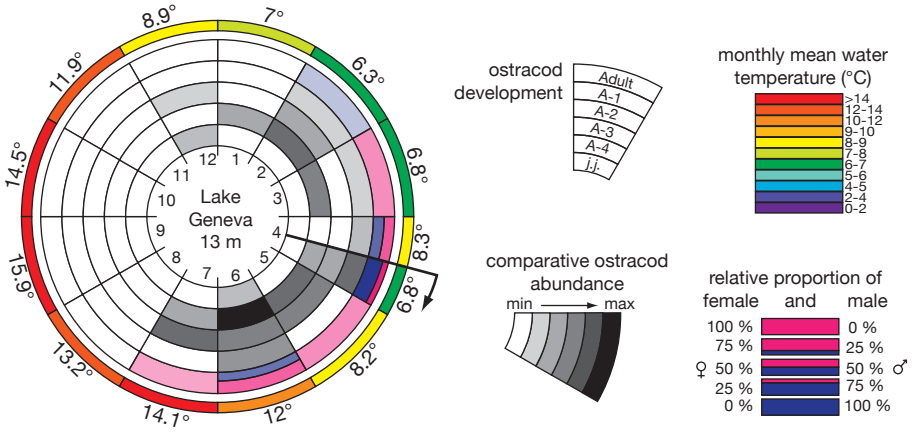

FIGURE AI.*Ls*.2
Life-cycle of *Limnocytherina sanctipatricii* at 13 m water depth illustrated with SOWM.

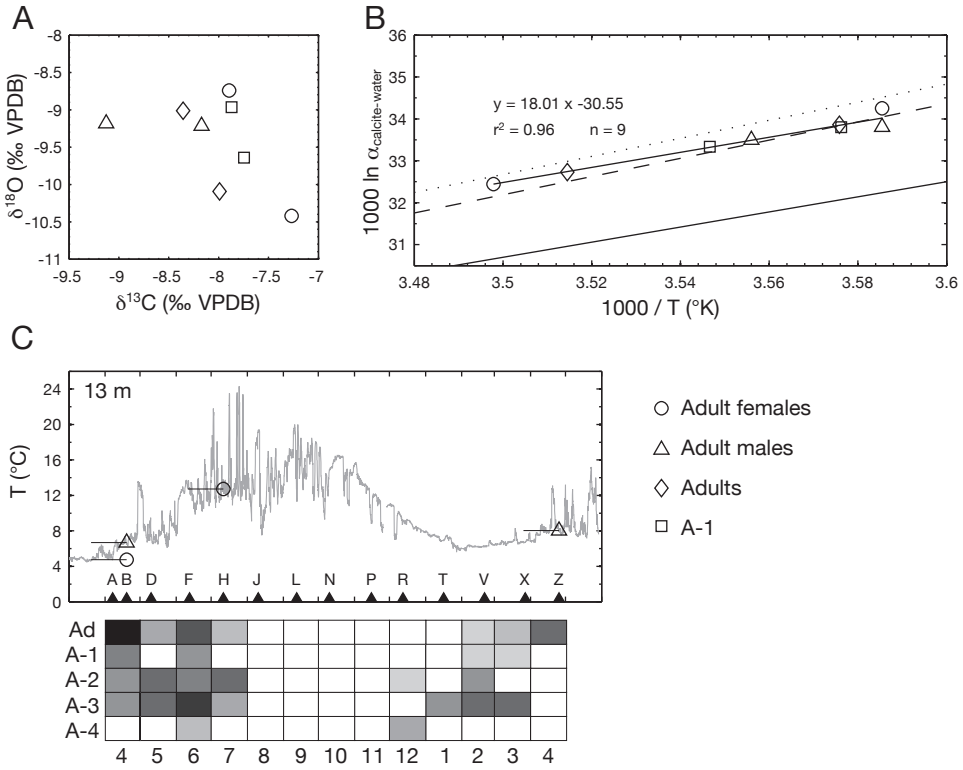

FIGURE AI.*Ls*.3
Oxygen isotope compositions of *Limnocytherina sanctipatricii* valves: oxygen versus carbon isotope compositions (A); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (B); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle at 13 m water depth (C).

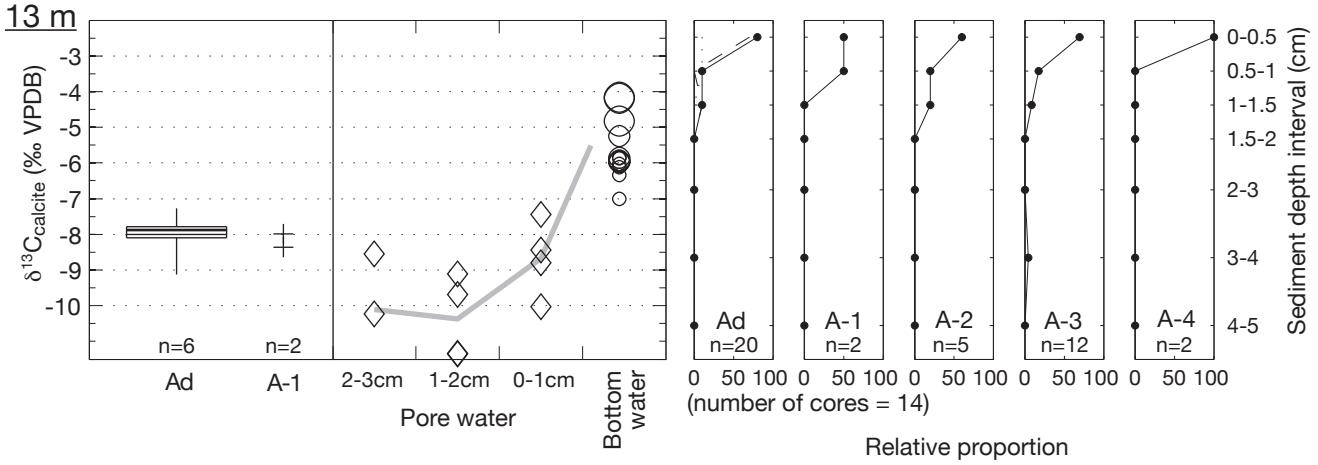

FIGURE AI.*Ls*.4
On the left side: carbon isotope compositions of *Limnocytherina sanctipatricii* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 13 water depth. On the right side: observed sediment penetration depths of *Limnocytherina sanctipatricii* at 13 m water depth. Dashed lines stand for females, dotted lines for males.

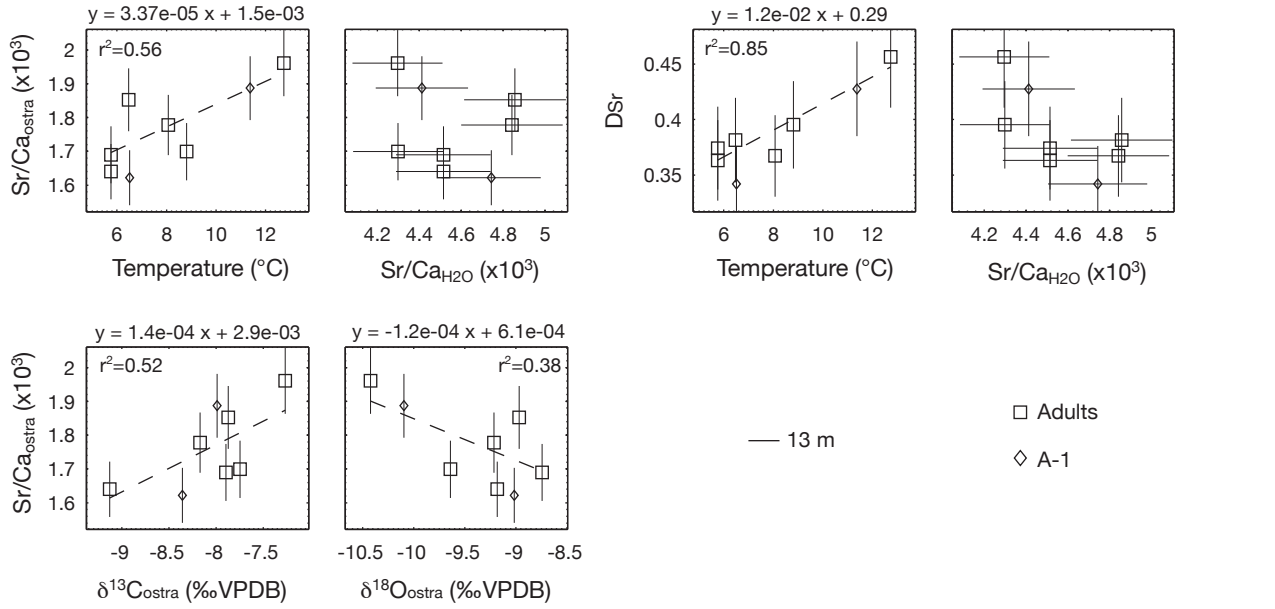

FIGURE AI.*Ls*.5
Sr/Ca and D_{Sr} of *Limnocytherina sanctipatricii* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions of the valves.

Cytherissa lacustris

(Sars, 1863)

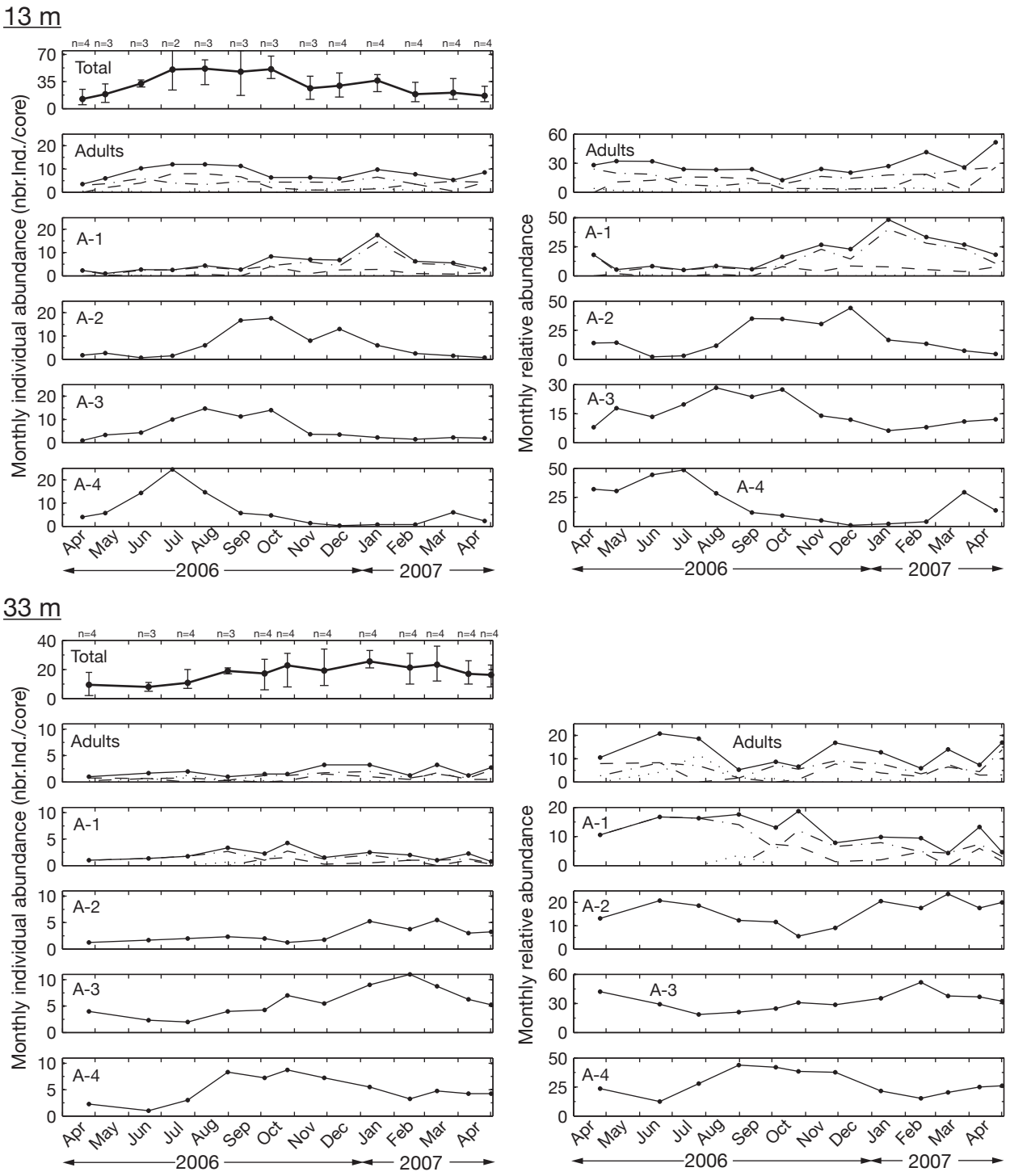

FIGURE AI.*Cl*.1a
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Cytherissa lacustris* at 13 and 33 m water depths. Dashed lines stand for clean specimes, dashed-dotted lines for relatively dirty specimes, dashed lines for very dirty specimens.

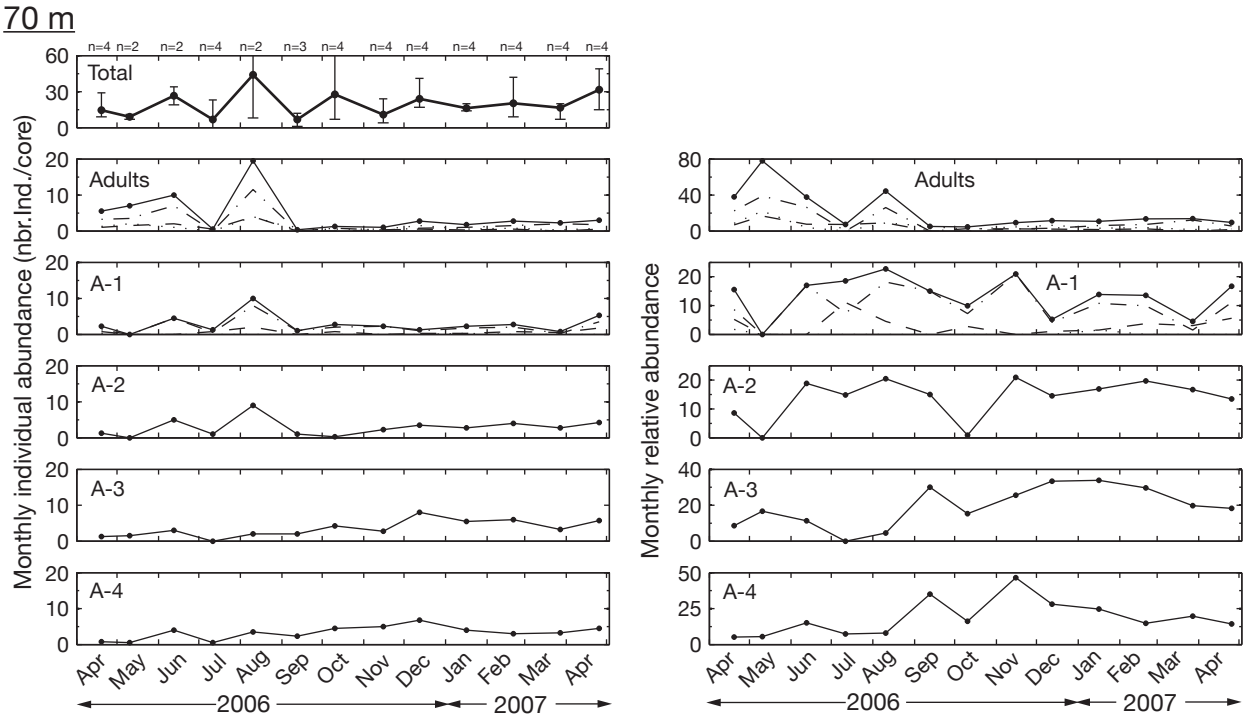

FIGURE AI.*Cl*.1b
Monthly individual abundances (left graphs) and monthly relative abundances (right graphs) of *Cytherissa lacustris* at 70 m water depth.

Cytherissa lacustris was mainly collected from 13 to 70 m depths. It is the most abundant species at the three deeper sites. Population density is 12000, 6600, and 6600 at 13, 33, and 70 m depths, respectively, representing 62, 72, and 64 % of the entire population at the same depths (Fig. 3.7).

Adults and juveniles of *C. lacustris* can be found throughout the year, but age structure as well as variation of abundance can be visualized on SOWM (Fig. 3.9). General appearance (shell transparency and dirtiness) was estimated for adults and A-1 juveniles to assess time span since moulting. This additional information (see Fig. AI.*Cl*.1) permits the identification of the period of active moulting (fresh specimens are symbolised by red "C", dirty with red "O" on SOWM in Fig. 3.9) and facilitates an understanding of the general pattern of the development. Life history is different at each depth. At 13 m, a general development trend can be recognised. Most A-4 juveniles appear in April and develop continuously to reach maturity in winter and spring. Most of the adults survive during these months. Development from instar A-4 to adult lasts 6 to 9 months, and adults can survive at least some 5 more months. At 33 m, development is distributed over the year and the trend is difficult to depict. Periods of active moulting (see red "C" on SOWM in Fig. 3.9) help to follow the individuals along their development. Maximum of A-4 is found in summer. These individuals reach stage A-3 in winter, stage A-2 in spring, stage A-1 at the end of spring and summer and attain maturity during the end of autumn and winter. At this depth, development from A-4 to adult lasts one to one and a half years. At 70 m depths, no development trend can be seen and old surviving individuals (red "O" in SOWM in Fig. 3.9) are found together with recently moulted adults, suggesting that different batches of adults overlap in time. At this depth, development of *C. lacustris* seems to have no seasonality.

This species does not appear to be such an active dweller (Fig. 3.10). Still, compared with the other data, *C. lacustris* ranks in the infaunal forms. To a first approximation, juveniles and adults present the same penetration depth. At 13 m, the population does not penetrate intensely into the sediment and about 50 % of the specimens were found in the top half-centimetre, 30-40 % in the half-centimetre underneath and the rest of the specimens mainly between 1 and 1.5 cm. In this site, the ability to dig increases slightly with age and younger juveniles tends to stay nearer the surface of the sediment, while adults go a little deeper. At 33 m depth, adults are mainly found near the surface, and a maximum of juveniles is found between 0.5 and 1.5 cm. Surprisingly, the capacity to dig is inverted

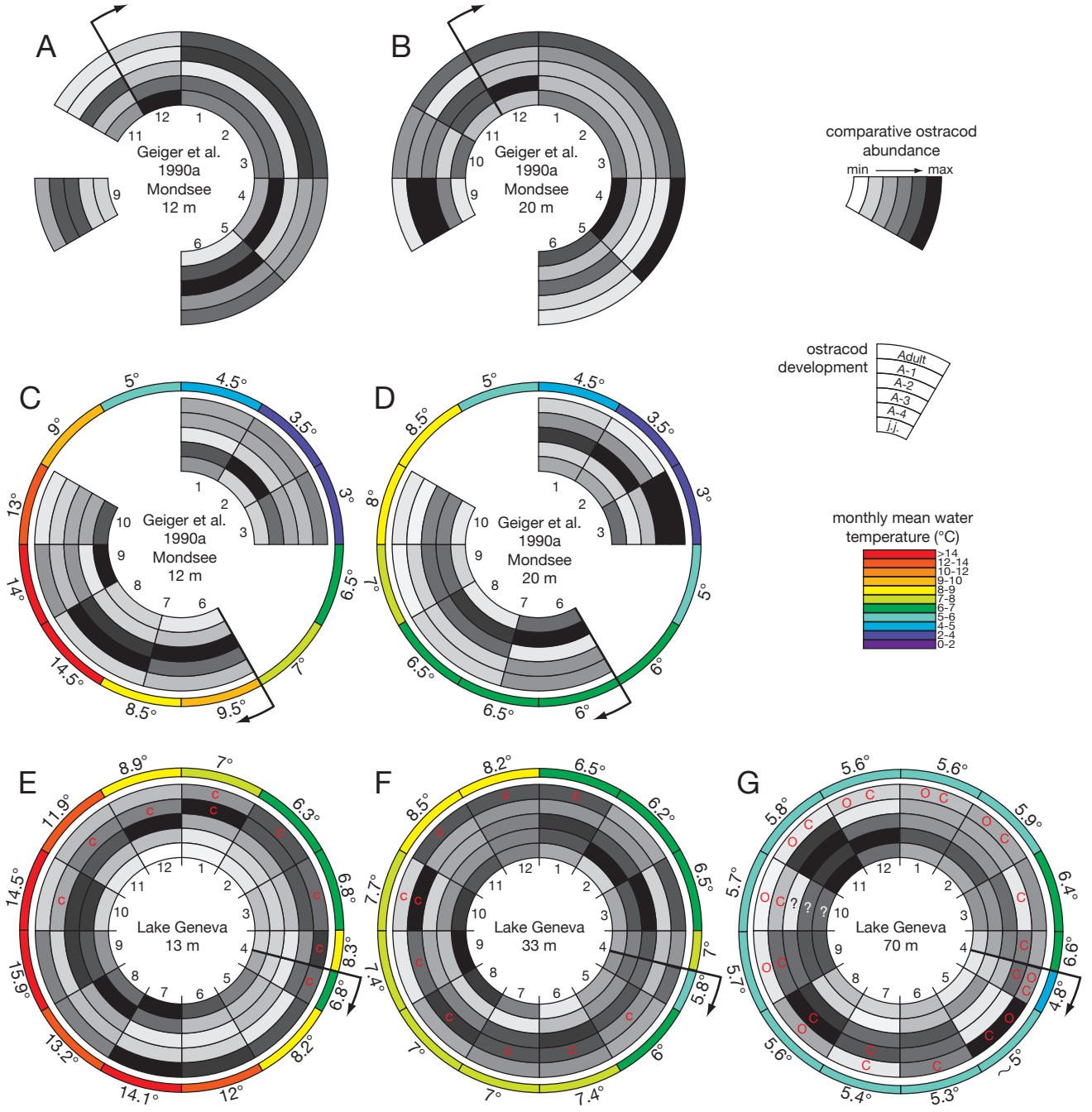

FIGURE AI.*Cl*.2
Life-cycles of *Cytherissa lacustris* in different localities illustrated with SOWM. Data from: Geiger et al., 1990a (A, B, C, and D); and present study (E, F, and G). Red C symbolise periods of crystallisation.

in comparison with the previous site. This behaviour is also observed at 70 m, where 50% of the specimens (i.e. adults and juveniles) are found between 0.5 and 1 cm, 25-30% in the top half-centimetre. Distribution of the rest of the population below 1 cm depends on the age. Adults are homogeneously distributed down to 3 cm, and the number of juveniles relative to adults increases with depths between 1 and 2 cm. Hence, the juveniles tend to be found deeper than adults but the latter are able to dig deeper than juveniles and can be found very deep in the sediment.

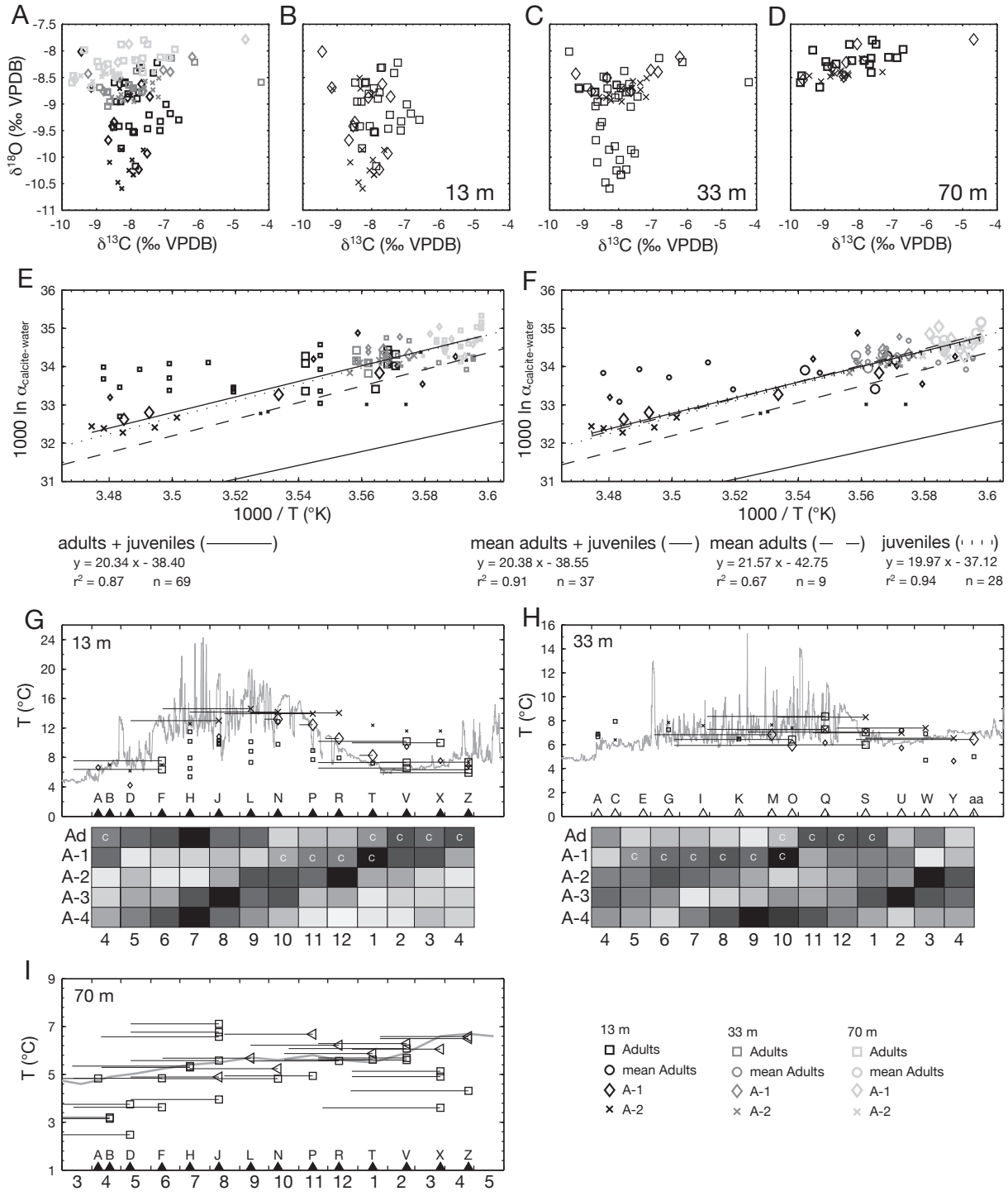

FIGURE AI.*Cl*.3
Oxygen isotope compositions of *Cytherissa lacustris* valves: oxygen versus carbon isotope compositions (A), same as A but for data at the different water depths (B, C, and D); oxygen isotope fractionation factors ($\alpha_{calcite\text{-}water}$) versus estimated temperatures of calcification (E); same as E but using monthly averages (F); water temperature and $\delta^{18}O$ recalculated calcification temperatures with subjacent illustration of the species life-cycle at 13 m water depth (G); same as for G but at 33 m water depth (H); same as G but at 70 m water depth without life-cycle illustration (I). White C symbolise periods of crystallisation.

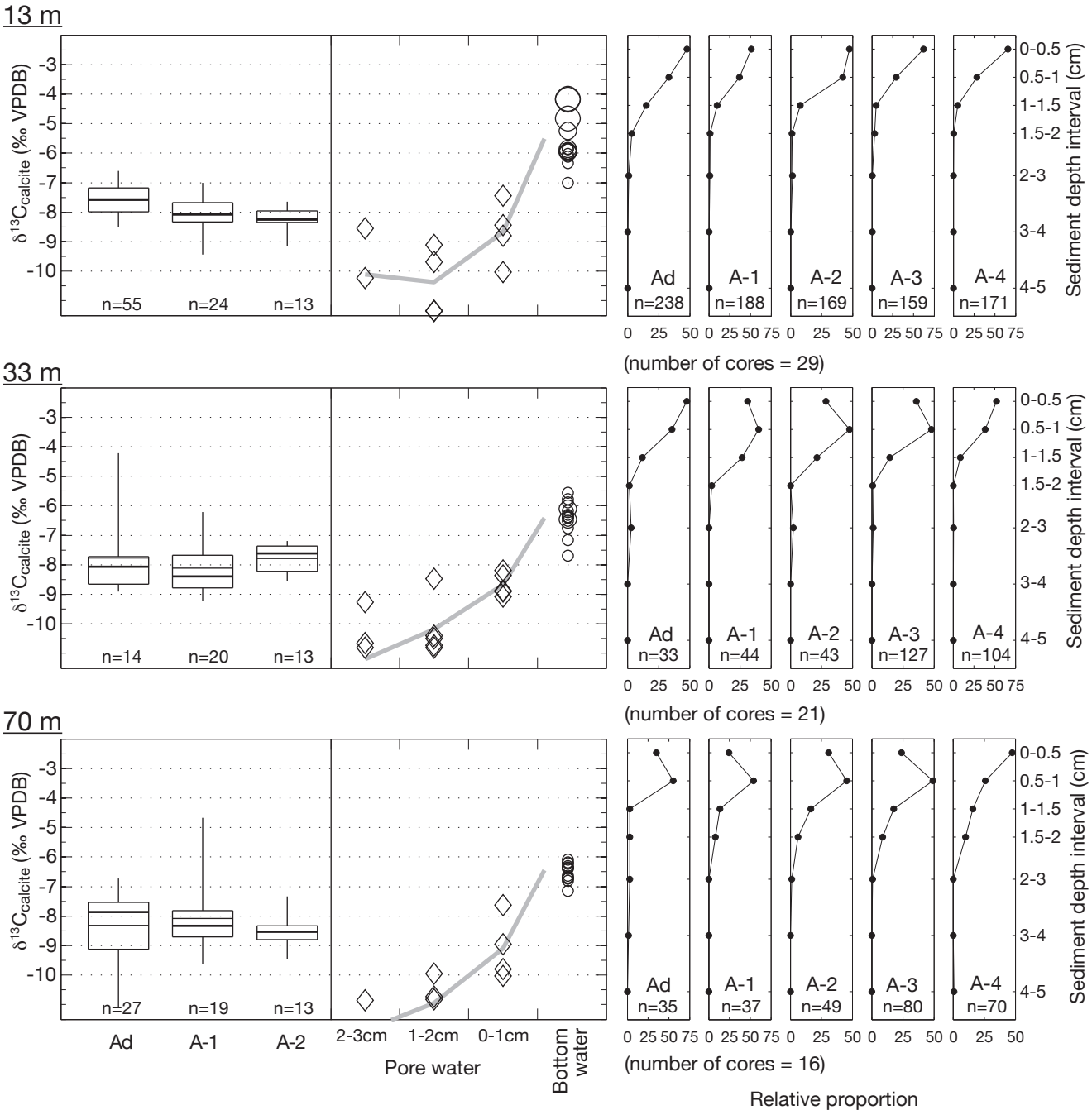

FIGURE AI.*Cl*.4
On the left side: carbon isotope compositions of *Cytherissa lacustris* valves and values for a calcite grown in equilibrium with DIC of bottom water and DIC of pore water at 13, 33 and 70 m water depths. On the right side: observed sediment penetration depths of *Cytherissa lacustris* at 13, 33 and 70 m water depths.

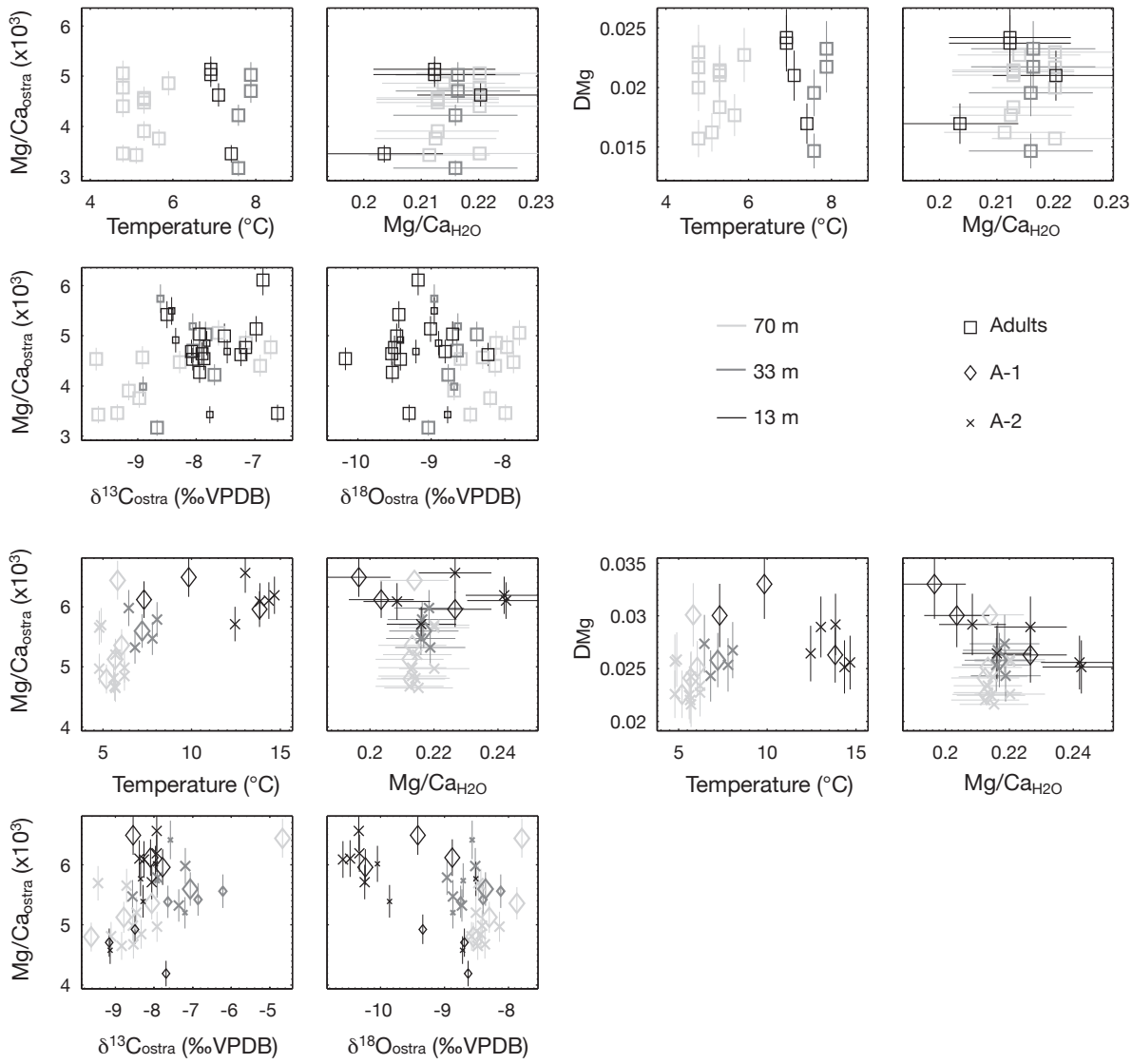

FIGURE AI.*Cl*.5a
Mg/Ca and D_{Mg} of adult and juvenile *Cytherissa lacustris* valves versus water temperature, Mg/Ca ratios of water and C- and O- isotope compositions of the valves.

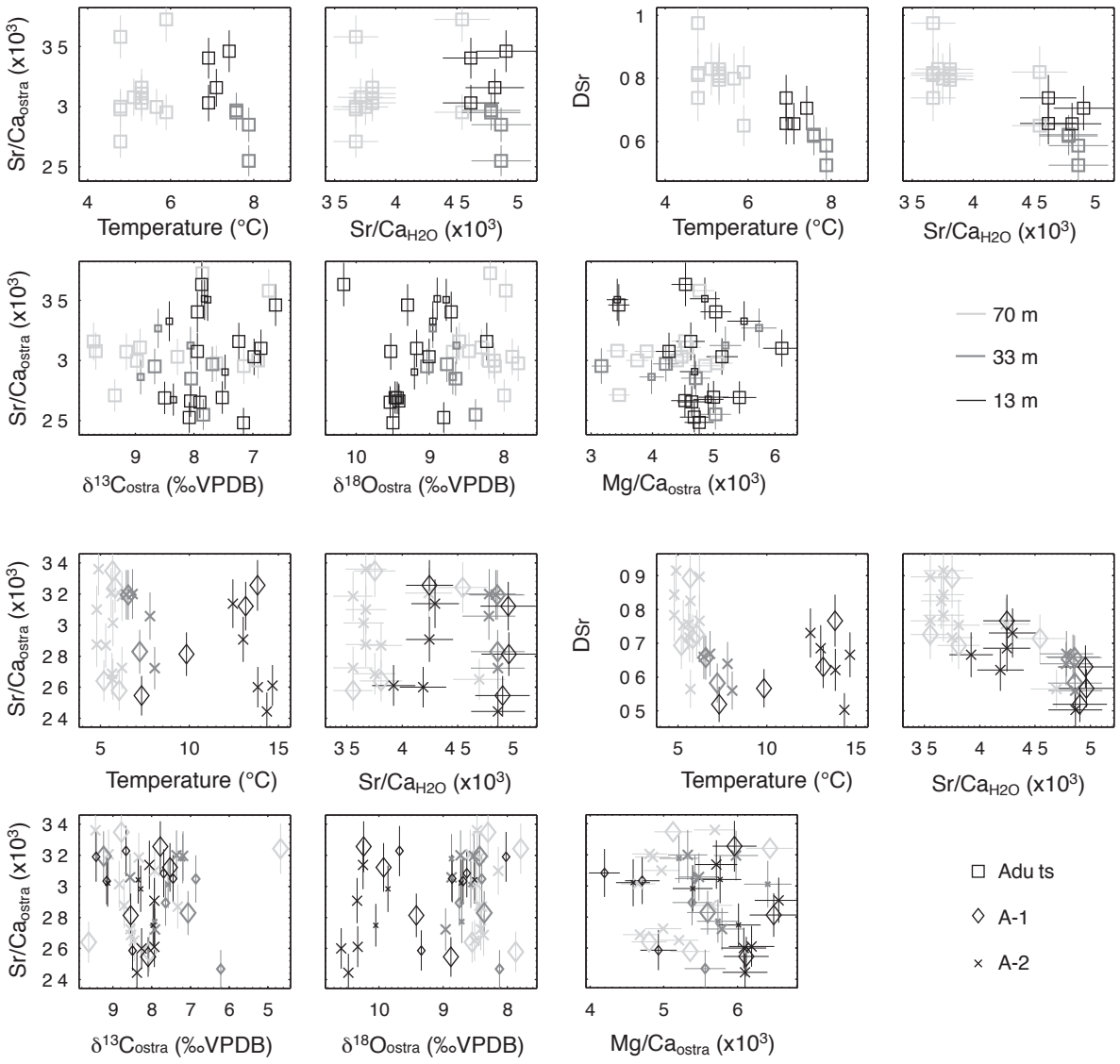

FIGURE AI.*Cl*.5b
Sr/Ca and D_{Sr} of adult and juvenile *Cytherissa lacustris* valves versus water temperature, Sr/Ca ratios of water and C- and O- isotope compositions as well as Mg/Ca ratios of the valves.

Cores LEBC

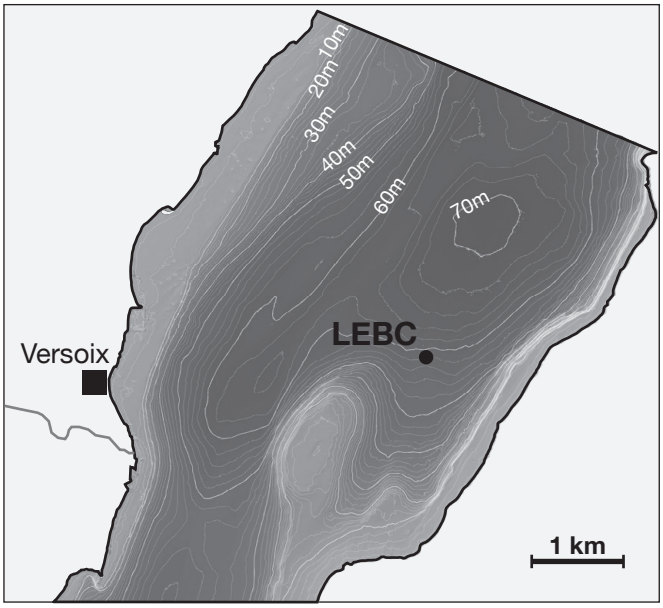

FIGURE AI.LEBC.1
Location of cores LEBC.

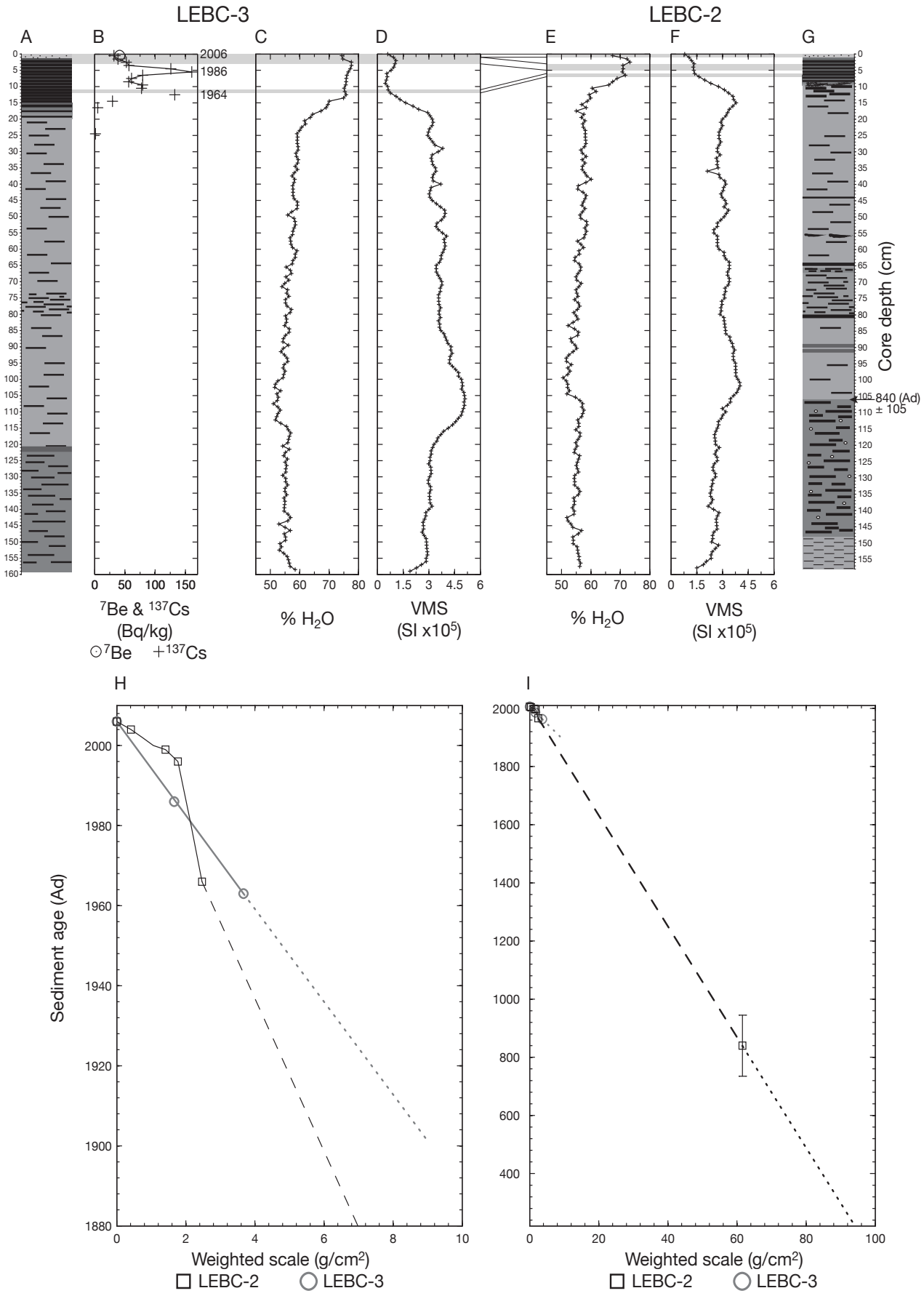

FIGURE AI.LEBC.2
Stratigraphic correlations between cores LEBC-2 and LEBC-3: Lithology LEBC-3 (A), ^{7}Be and ^{137}Cs LEBC-3 (B), wt % H_2O LEBC-3 (C), Volumic magnetic susceptibility (VMS) LEBC-3 (D), wt % H_2O LEBC-2 (E), VMS LEBC-2 (F), Lithology LEBC-2 with one ^{14}C age in calendar years at 105.5 cm (G), Age models for LEBC-2 and LEBC-3 (H and I).

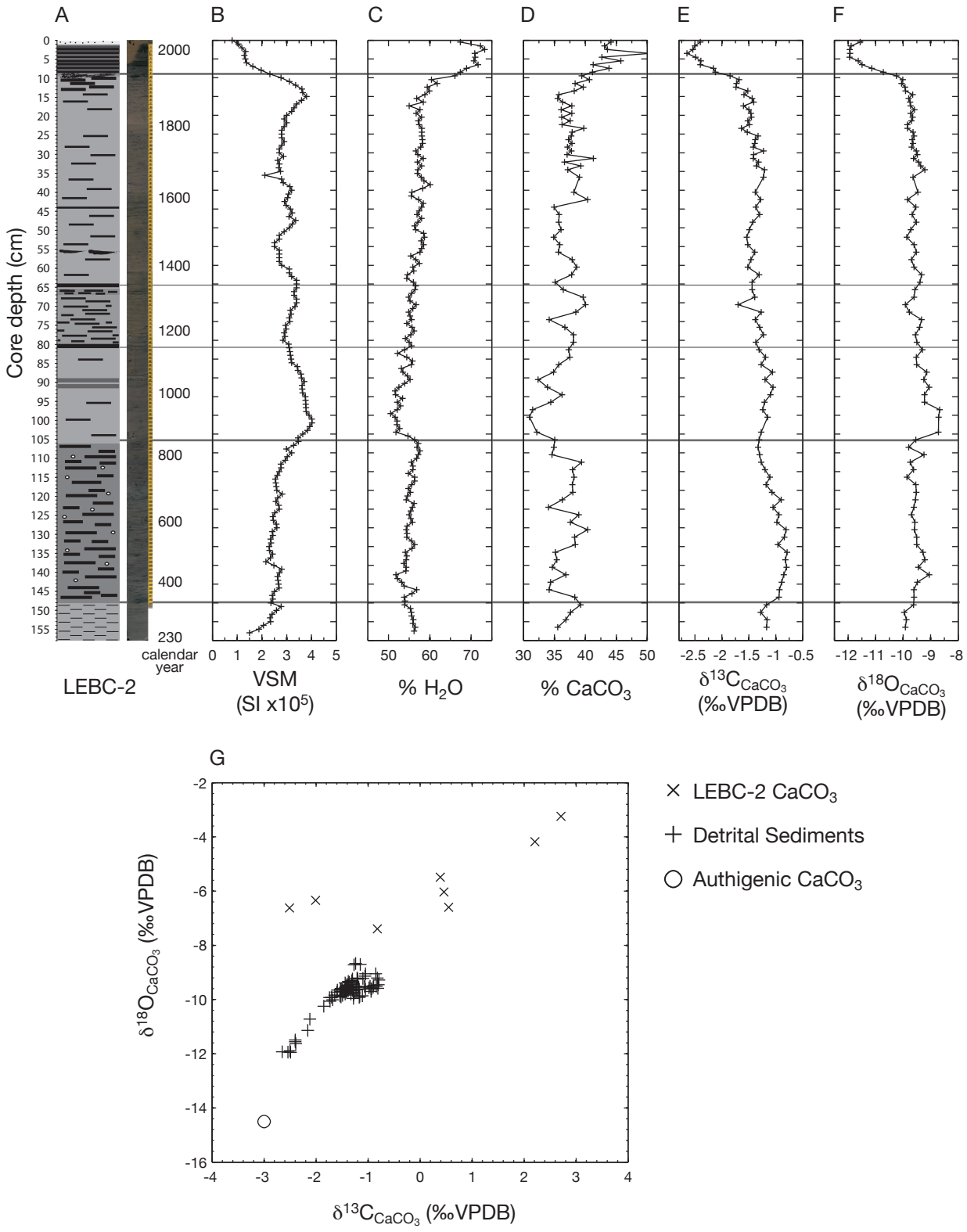

FIGURE AI.LEBC.3
Sediment geochemistry of core LEBC-2: Lithology (A), Water content (B), Volumic magnetic susceptibility (C), Carbonate dried weight content (D), bulk carbonate $\delta^{13}C$ values (E) and $\delta^{18}O$ values (F), and bulk carbonate $\delta^{18}O$ values plottet against $\delta^{13}C$ values (G).

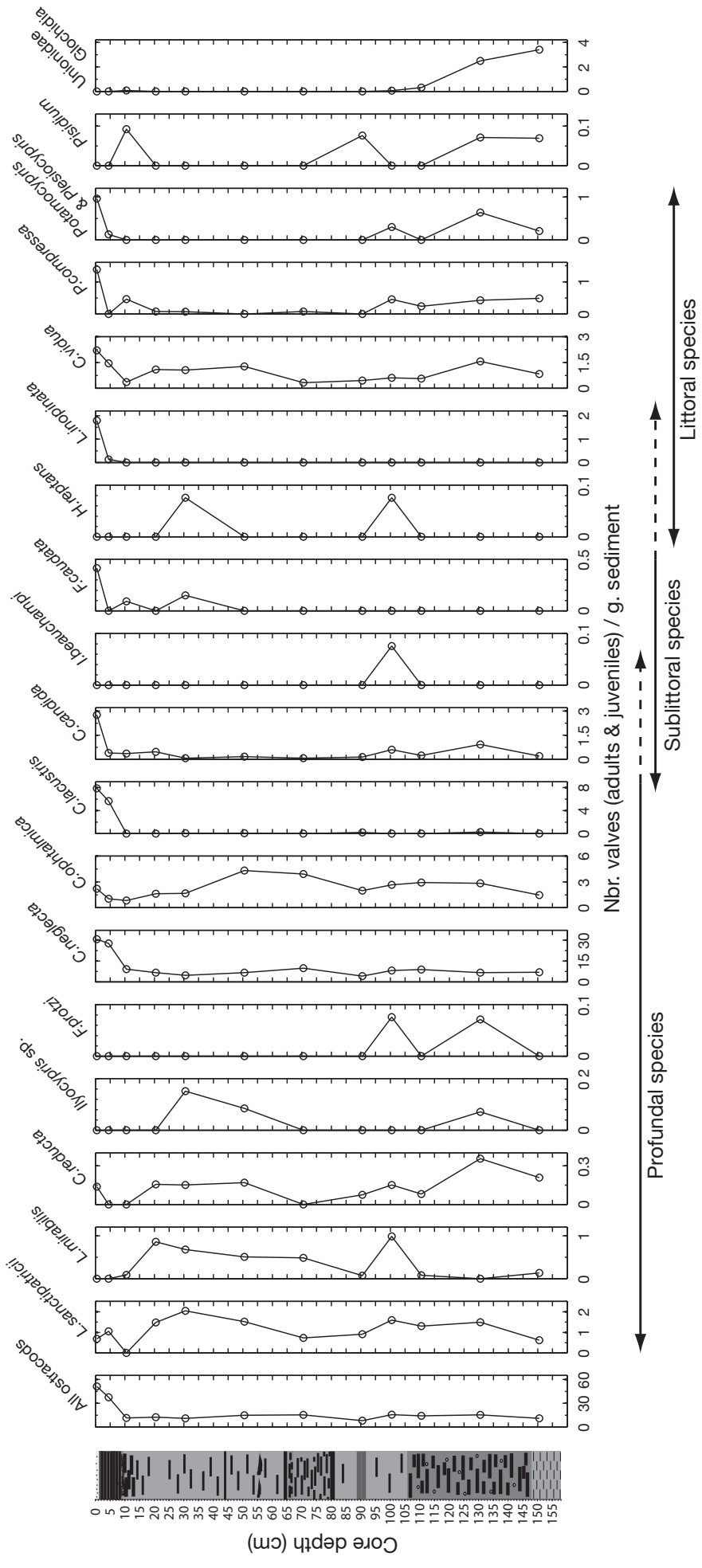

FIGURE AI.LEBC.4
Ostracod fossil assemblages of core LEBC-2.

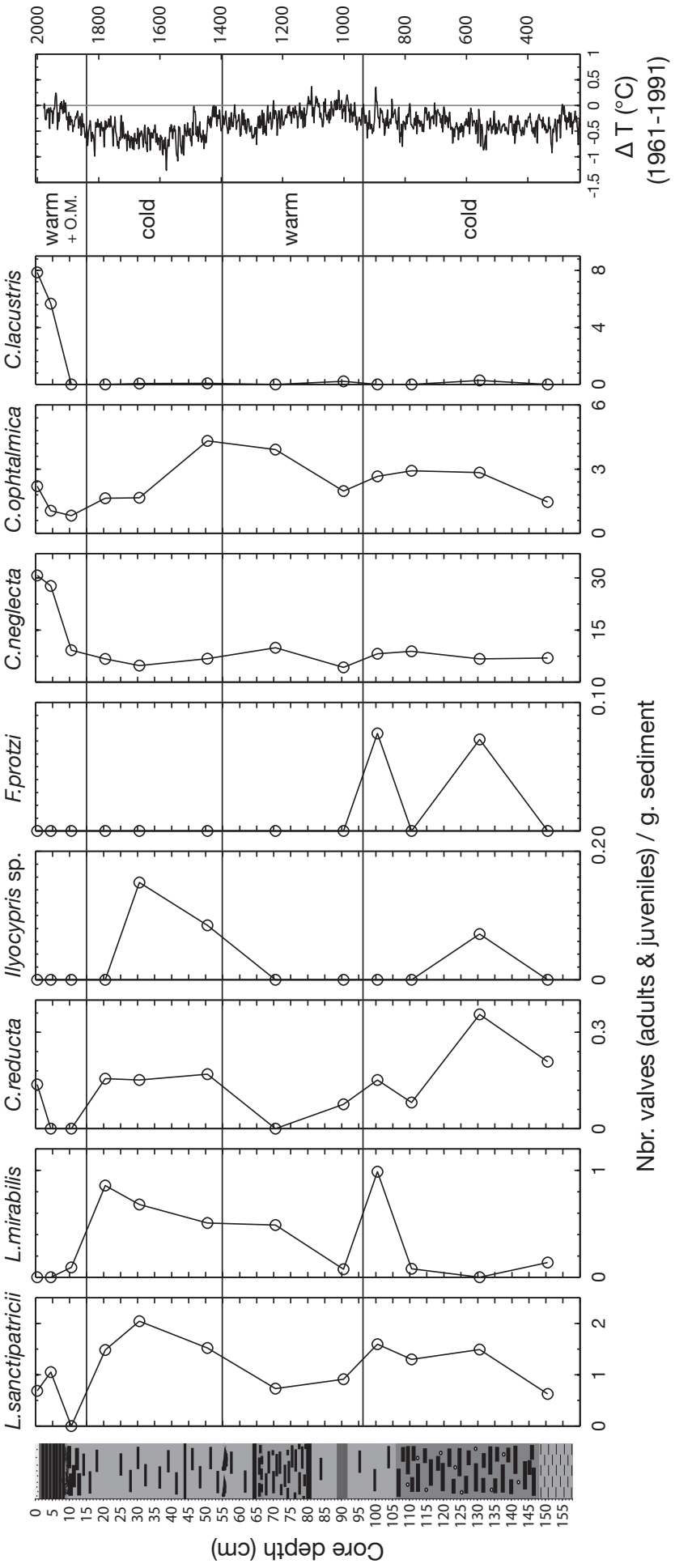

FIGURE AI.LEBC.5
Profundal species versus climatic evolution (from Moberg et al., 2005)

APPENDIX II

Ostracod ecology

Geochemistry *Candonidae*

Geochemistry *Cyprididae*

Geochemistry *Cytheroidea*

TABLE AII-1
Ostracod monthly abundances; *Candona candida*.

species	site	sampling date	total abund.	std	max	min	nbr. of cores	female adultes	male adultes	female A-1	male A-2	A-2	A-3	A-4	A-5	A-6
Candona candida	13 m	04.19.06	0.00	0.00	0	0	5	0.00		0.00		0.00	0.00	0.00	-	-
		05.10.06	0.00	0.00	0	0	3	0.00		0.00		0.00	0.00	0.00	-	-
		06.12.06	2.67	3.79	7	0	3	0.33		0.00		1.67	0.67	0.00	-	-
		07.11.06	3.50	3.54	6	1	2	0.00		0.00		3.50	0.00	0.00	-	-
		08.10.06	2.25	1.89	5	1	4	0.00		0.00		1.75	0.50	0.00	-	-
		09.12.06	2.00	2.00	4	0	3	0.00		0.00		2.00	0.00	0.00	-	-
		10.10.06	1.75	1.71	4	0	4	0.00		0.00		1.75	0.00	0.00	-	-
		11.15.06	2.33	2.08	4	0	3	0.67		1.67		0.00	0.00	0.00	-	-
		12.12.06	1.00	1.00	2	0	3	0.33		0.67		0.00	0.00	0.00	-	-
		01.16.07	0.50	1.00	2	0	4	0.25		0.25		0.00	0.00	0.00	-	-
		02.20.07	0.00	0.00	0	0	4	0.00		0.00		0.00	0.00	0.00	-	-
		03.27.07	0.25	0.50	1	0	4	0.25		0.00		0.00	0.00	0.00	-	-
		04.25.07	0.50	0.58	1	0	4	0.00		0.00		0.00	0.00	0.50	-	-
		annual population density = 1.3 ind./core (=490 ind./m^2)														
		annual maximum = 3.5 ind./core (=1300 ind./m^2)														
	33 m	04.25.06	0.00	0.00	0	0	4	0.00		0.00		0.00	0.00	0.00	-	-
		06.19.06	0.33	0.58	1	0	3	0.00		0.00		0.00	0.00	0.33	-	-
		07.25.06	2.00	2.16	5	0	4	0.00		0.00		0.50	1.25	0.25	-	-
		08.31.06	1.00	1.00	2	0	3	0.00		0.00		1.00	0.00	0.00	-	-
		10.04.06	1.00	0.82	2	0	4	0.00		0.50		0.50	0.00	0.00	-	-
		10.25.06	1.50	0.58	2	1	4	0.50		0.75		0.25	0.00	0.00	-	-
		11.28.06	0.75	0.50	1	0	4	0.75		0.00		0.00	0.00	0.00	-	-
		01.09.07	1.00	1.15	2	0	4	1.00		0.00		0.00	0.00	0.00	-	-
		02.15.07	0.75	0.50	1	0	4	0.75		0.00		0.00	0.00	0.00	-	-
		03.12.07	0.25	0.50	1	0	4	0.25		0.00		0.00	0.00	0.00	-	-
		04.10.07	0.25	0.50	1	0	4	0.25		0.00		0.00	0.00	0.00	-	-
		05.01.07	0.25	0.50	1	0	4	0.25		0.00		0.00	0.00	0.00	-	-
		annual population density = 0.8 ind./core (=290 ind./m^2)														
		annual maximum = 2.0 ind./core (=760 ind./m^2)														

TABLE AII-1
Continuation; *Candona neglecta*.

species	site	sampling date	total abund.	std	max	min	nbr. of cores	female adultes	male adultes	female A-1	male A-2	A-2	A-3	A-4	A-5	A-6
Candona neglecat	13 m	04.19.06	2.50	1.91	5	1	4	1.75	0.25	0.00	0.00	0.25	0.00	0.25	-	-
		05.10.06	1.00	0.00	1	1	2	0.50	0.00	0.00	0.00	0.00	0.00	0.50	-	-
		06.12.06	0.50	0.58	1	0	4	0.00	0.00	0.00	0.00	0.00	0.25	0.25	-	-
		07.11.06	11.0	5.66	15	7	2	0.00	0.00	0.00	0.00	6.00	4.50	0.50	-	-
		08.10.06	16.7	9.02	26	8	3	0.00	0.00	0.00	0.00	14.3	2.33	0.00	-	-
		09.12.06	11.7	7.09	18	4	3	0.00	0.00	0.00	0.00	11.7	0.00	0.00	-	-
		10.10.06	13.5	6.86	22	7	4	0.00	0.00	0.00	0.00	13.3	0.25	0.00	-	-
		11.15.06	4.00	6.08	11	0	3	0.00	0.00	0.00	0.33	3.67	0.00	0.00	-	-
		12.12.06	11.5	3.11	16	9	4	0.50	1.25	1.75	0.75	7.25	0.00	0.00	-	-
		01.16.07	14.0	5.29	19	7	4	3.75	2.00	1.75	1.00	5.50	0.00	0.00	-	-
		02.19.07	4.25	1.50	6	3	4	2.25	0.50	0.50	0.50	0.50	0.00	0.00	-	-
		03.27.07	4.50	3.70	9	1	4	2.75	1.25	0.25	0.00	0.00	0.00	0.25	-	-
		04.25.07	1.00	1.41	3	0	4	0.50	0.25	0.00	0.00	0.25	0.00	0.00	-	-
		annual population density = 7.4 ind./core (=2800 ind./m^2)						annual productivity = 12 ind.								
		annual maximum = 16.7 ind./core (=6300 ind./m^2)						net productivity = 1.71 ind./month								
	33 m	04.25.06	5.00	1.41	7	4	4	0.50	1.50	1.00	0.25	1.50	0.25	0.00	-	-
		06.19.06	6.00	1.73	8	5	3	3.00	0.33	0.33	0.67	0.67	1.00	0.00	-	-
		07.25.06	3.25	2.87	7	1	4	2.00	0.25	0.50	0.25	0.25	0.00	0.00	-	-
		08.31.06	3.67	2.08	6	2	3	2.00	0.00	0.33	0.00	0.33	0.33	0.67	-	-
		10.04.06	3.25	1.50	5	2	4	1.50	0.00	0.00	0.00	1.00	0.50	0.25	-	-
		10.25.06	2.25	2.06	5	0	4	1.25	0.00	0.00	0.25	0.75	0.00	0.00	-	-
		11.28.06	4.25	0.50	5	4	4	0.50	0.00	0.00	0.00	2.00	0.50	1.25	-	-
		01.09.07	7.25	4.79	14	3	4	0.75	0.00	0.75	0.00	2.25	2.25	1.25	-	-
		02.15.07	10.0	6.06	16	3	4	0.00	0.00	0.25	0.25	5.75	2.25	1.50	-	-
		03.12.07	8.50	3.79	11	3	4	0.75	0.50	2.75	0.50	2.50	1.50	0.00	-	-
		04.10.07	8.50	3.00	11	5	4	0.50	0.75	1.25	1.50	2.50	1.50	0.50	-	-
		05.01.07	7.00	2.16	9	4	4	0.75	1.00	2.25	0.50	1.75	0.75	0.00	-	-
		annual population density = 5.74 ind./core (=2200 ind./m^2)						annual productivity = 14 ind.								
		annual maximum = 10.0 ind./core (=3800 ind./m^2)						net productivity = 1.23 ind./month								
	70 m	04.19.06	6.75	2.87	10	3	4	0.25	0.25	1.00	0.25	1.25	2.00	1.75	-	-
		05.10.06	8.00	5.66	12	4	2	1.00	0.00	0.50	1.00	1.00	3.50	1.00	-	-
		06.12.06	8.00	4.24	11	5	2	2.00	1.50	0.00	1.00	2.00	1.50	0.00	-	-
		07.15.06	6.75	7.59	17	1	4	1.50	0.75	0.25	0.75	2.25	1.00	0.25	-	-
		08.23.06	18.5	19.1	32	5	2	2.50	4.50	2.00	2.00	7.00	0.50	0.00	-	-
		09.12.06	9.33	0.58	10	9	3	1.67	2.00	2.00	0.67	2.00	0.00	1.00	-	-
		10.10.06	8.00	4.69	12	3	4	2.50	2.00	2.00	0.00	1.00	0.00	0.50	-	-
		11.15.06	3.25	1.71	5	1	4	2.25	0.50	0.25	0.00	0.00	0.00	0.25	-	-
		12.12.06	3.25	1.71	5	1	4	2.25	0.50	0.25	0.00	0.00	0.00	0.25	-	-
		01.16.07	9.25	2.75	12	6	4	3.00	0.75	0.75	0.50	0.25	1.75	2.25	-	-
		02.19.07	8.00	4.16	13	3	4	1.75	0.75	0.50	0.25	1.75	1.50	1.50	-	-
		03.27.07	7.50	5.57	15	2	4	1.75	0.00	0.25	0.50	0.75	2.75	1.50	-	-
		04.25.07	7.50	3.70	11	3	4	0.25	0.50	1.00	1.00	1.50	2.50	0.75	-	-
		annual population density = 7.1 ind./core (=2700 ind./m^2)						annual productivity = 20 ind.								
		annual maximum = 9.3 ind./core (=3500 ind./m^2)						net productivity = 1.74 ind./month								

TABLE AII-1
Continuation; *Fabaeformiscandona compressa* and *Pseudocandona compressa*.

species	site	sampling date	total abund.	std	max	min	nbr. of cores	female adultes	male adultes	female A-1	male A-2	A-2	A-3	A-4	A-5	A-6
Fabae-formiscandona caudata	13 m	04.19.06	1.40	2.07	5	0	5	0.40		0.40		0.20	0.00	0.40	-	-
		05.10.06	4.00	3.00	7	1	3	1.67		0.00		0.00	1.00	1.33	-	-
		06.12.06	4.00	2.08	6	2	3	1.00		0.33		2.00	0.33	0.00	-	-
		07.11.06	3.50	0.71	4	3	3	0.00		0.50		2.50	1.00	0.00	-	-
		08.10.06	4.33	1.53	6	3	3	0.33		0.33		3.33	0.33	0.00	-	-
		09.12.06	3.00	4.36	8	0	3	0.00		0.00		3.00	0.00	0.00	-	-
		10.10.06	6.00	4.00	12	4	4	0.00		0.50		5.50	0.00	0.00	-	-
		11.15.06	2.33	1.15	3	1	3	0.00		0.00		2.33	0.00	0.00	-	-
		12.12.06	4.00	3.65	8	0	4	0.50		0.75		2.75	0.00	0.00	-	-
		01.16.07	5.75	3.77	11	2	4	0.75		0.00		5.00	0.00	0.00	-	-
		02.19.07	2.75	2.06	5	0	4	0.00		0.00		2.75	0.00	0.00	-	-
		03.27.07	2.75	1.71	5	1	4	0.25		0.75		1.75	0.00	0.00	-	-
		04.25.07	1.25	0.50	2	1	4	0.75		0.00		0.50	0.00	0.00	-	-
		annual population density = 3.5 ind./core (=1300 ind./m^2)														
		annual maximum = 6.0 ind./core (=2300 ind./m^2)														
Pseudocandona compressa	2 m[a)]	04.07.06	0	-	-	-	-	0	0	0	0	0	-	-	-	-
		04.25.06	35	-	-	-	-	23	7	2	0	3	-	-	-	-
		05.24.06	7	-	-	-	-	4	2	0	1	0	-	-	-	-
		06.19.06	12	-	-	-	-	7	1	2	0	2	-	-	-	-
		07.25.06	13	-	-	-	-	7	0	0	0	6	-	-	-	-
		08.31.06	9	-	-	-	-	5	0	0	0	4	-	-	-	-
		10.04.06	1	-	-	-	-	1	0	0	0	0	-	-	-	-
		10.25.06	30	-	-	-	-	0	0	0	0	30	-	-	-	-
		11.28.06	20	-	-	-	-	1	0	0	0	19	-	-	-	-
		01.09.07	50	-	-	-	-	0	0	0	0	50	-	-	-	-
		02.15.07	50	-	-	-	-	0	0	0	0	50	-	-	-	-
		03.12.07	68	-	-	-	-	0	1	5	7	55	-	-	-	-
		04.10.07	24	-	-	-	-	3	8	9	2	2	-	-	-	-
		05.01.07	193	-	-	-	-	147	45	0	1	0	-	-	-	-
	5 m[a)]	04.07.06	104	-	-	-	-	1	3	27	21	52	0	-	-	-
		04.25.06	231	-	-	-	-	43	30	56	15	87	0	-	-	-
		05.24.06	61	-	-	-	-	46	5	1	1	8	0	-	-	-
		06.19.06	101	-	-	-	-	86	8	1	1	5	0	-	-	-
		07.25.06	386	-	-	-	-	96	63	18	6	164	39	-	-	-
		08.31.06	111	-	-	-	-	11	2	0	0	73	25	-	-	-
		10.04.06	164	-	-	-	-	2	2	0	0	154	6	-	-	-
		10.25.06	200	-	-	-	-	0	0	0	0	200	0	-	-	-
		11.28.06	206	-	-	-	-	5	0	1	0	200	0	-	-	-
		01.09.07	200	-	-	-	-	0	0	0	0	200	0	-	-	-
		02.15.07	208	-	-	-	-	1	0	2	5	200	0	-	-	-
		03.12.07	209	-	-	-	-	1	1	7	0	200	0	-	-	-
		04.10.07	295	-	-	-	-	16	31	100	53	95	0	-	-	-
		05.01.07	254	-	-	-	-	155	45	27	3	24	0	-	-	-

TABLE AII-1
Continuation; *Cypria ophtalmica* forma *lacustris*.

species	site	sampling date	total abund.	std	max	min	nbr. of cores	adults	juveniles
Cypria ophtalmica forma *lacustris*[b)]	13 m	04.19.06	0.20	0.45	1	0	4	0.20	0.00
		05.10.06	3.50	4.04	7	0	2	3.00	0.50
		06.12.06	4.67	7.23	13	0	3	4.00	0.67
		07.11.06	1.00	1.41	2	0	2	1.00	0.00
		08.10.06	7.33	5.00	12	2	3	3.67	3.67
		09.12.06	2.00	2.65	5	0	3	2.00	0.00
		10.10.06	3.00	1.00	4	2	3	3.00	0.00
		11.15.06	2.00	2.65	5	0	3	2.00	0.00
		12.12.06	2.00	1.41	4	1	4	2.00	0.00
		01.16.07	0.75	0.96	2	0	4	0.50	0.25
		02.19.07	2.75	1.26	4	1	4	2.75	0.00
		03.27.07	5.00	3.65	9	1	4	4.50	0.50
		04.25.07	3.75	4.35	10	0	4	3.50	0.25
		annual population density = 2.9 ind./core (=970 ind./m^2)							
		annual maximum = 7.3 ind./core (=2800 ind./m^2)							
	33 m	04.25.06	0.25	0.50	1	0	4	0.25	-
		06.19.06	0.67	1.15	2	0	3	0.67	-
		07.25.06	0.00	0.00	0	0	4	0.00	-
		08.31.06	0.00	0.00	0	0	3	0.00	-
		10.04.06	0.00	0.00	0	0	4	0.00	-
		10.25.06	0.00	0.00	0	0	4	0.00	-
		11.28.06	0.50	1.00	2	0	4	0.50	-
		01.09.07	0.00	0.00	0	0	4	0.00	-
		02.15.07	0.25	0.50	1	0	4	0.25	-
		03.12.07	0.50	1.00	2	0	4	0.50	-
		04.10.07	0.25	0.50	1	0	4	0.25	-
		05.01.07	0.00	0.00	0	0	4	0.00	-
		annual population density = 0.2 ind./core (=76 ind./m^2)							
		annual maximum = 0.7 ind./core (=250 ind./m^2)							
	70 m	04.19.06	16.0	8.49	22	10	2	16.0	0.00
		05.10.06	12.5	14.8	23	2	2	12.0	0.50
		06.12.06	12.5	14.8	23	2	2	12.0	0.50
		07.15.06	1.25	0.96	2	0	4	1.25	0.00
		08.23.06	3.50	0.71	4	3	2	3.00	0.50
		09.12.06	1.33	0.58	2	1	3	1.00	0.33
		10.10.06	5.00	2.83	9	3	4	3.25	1.75
		11.15.06	2.75	2.06	5	0	4	2.50	0.25
		12.12.06	11.0	7.16	18	3	4	9.75	1.25
		01.16.07	8.75	9.46	22	1	4	8.25	0.50
		02.19.07	4.25	0.96	5	3	4	3.50	0.75
		03.27.07	10.5	10.1	25	2	4	9.75	0.75
		04.25.07	4.75	5.19	12	1	4	4.50	0.25
		annual population density = 7.5 ind./core (=2700 ind./m^2)							
		annual maximum = 16 ind./core (=6100 ind./m^2)							

TABLE AII-1
Continuation; *Herpetocypris reptans*.

species	site	sampling date	total abund.	std	max	min	nbr. of cores	female adultes	male adultes	female A-1	male A-2	A-2	A-3	A-4	A-5	A-6
Herpetocypris reptans	2 m[a)]	04.07.06	0	-	-	-	-	0		0		0	0	0	0	0
		04.25.06	0	-	-	-	-	0		0		0	0	0	0	0
		05.24.06	2	-	-	-	-	0		0		0	1	1	0	0
		06.19.06	1	-	-	-	-	0		1		0	0	0	0	0
		07.25.06	1	-	-	-	-	0		0		0	0	0	1	0
		08.31.06	0	-	-	-	-	0		0		0	0	0	0	0
		10.04.06	0	-	-	-	-	0		0		0	0	0	0	0
		10.25.06	1	-	-	-	-	1		0		0	0	0	0	0
		11.28.06	1	-	-	-	-	0		0		1	0	0	0	0
		01.09.07	4	-	-	-	-	3		0		1	0	0	0	0
		02.15.07	1	-	-	-	-	1		0		0	0	0	0	0
		03.12.07	2	-	-	-	-	2		0		0	0	0	0	0
		04.10.07	0	-	-	-	-	0		0		0	0	0	0	0
		05.01.07	18	-	-	-	-	2		0		0	3	13	0	0
	5 m[a)]	04.07.06	2	-	-	-	-	1		0		0	1	0	0	0
		04.25.06	3	-	-	-	-	3		0		0	0	0	0	0
		05.24.06	0	-	-	-	-	0		0		0	0	0	0	0
		06.19.06	0	-	-	-	-	0		0		0	0	0	0	0
		07.25.06	1	-	-	-	-	1		0		0	0	0	0	0
		08.31.06	0	-	-	-	-	0		0		0	0	0	0	0
		10.04.06	1	-	-	-	-	0		0		1	0	0	0	0
		10.25.06	8	-	-	-	-	5		3		0	0	0	0	0
		11.28.06	2	-	-	-	-	2		0		0	0	0	0	0
		01.09.07	2	-	-	-	-	2		0		0	0	0	0	0
		02.15.07	2	-	-	-	-	2		0		0	0	0	0	0
		03.12.07	0	-	-	-	-	0		0		0	0	0	0	0
		04.10.07	2	-	-	-	-	2		0		0	0	0	0	0
		05.01.07	7	-	-	-	-	1		0		1	1	4	0	0
	13 m	04.19.06	2.80	4.21	10	0	5	1.20		0.80		0.00	0.00	0.00	0.00	0.00
		05.10.06	0.67	0.58	1	0	3	0.33		0.33		0.00	0.00	0.00	0.00	0.00
		06.12.06	3.50	1.91	6	2	2	0.75		0.00		0.00	0.00	0.50	1.25	1.00
		07.11.06	6.33	5.51	10	0	3	0.33		0.00		2.67	2.00	0.33	0.67	0.33
		08.10.06	3.50	1.83	6	2	4	0.25		1.50		0.00	0.00	1.00	1.25	0.00
		09.12.06	2.00	1.00	3	1	3	1.33		0.33		0.00	0.33	0.00	0.00	0.00
		10.10.06	2.50	0.58	3	2	4	1.25		0.00		0.25	0.50	0.50	0.00	0.00
		11.15.06	3.00	2.65	5	0	3	1.33		0.67		0.33	0.33	0.33	0.00	0.00
		12.12.06	2.50	1.29	4	1	4	0.75		0.25		0.25	0.00	0.50	0.25	0.50
		01.17.07	2.75	0.96	4	2	4	0.75		0.00		0.00	0.25	0.50	1.00	0.25
		02.19.07	2.50	0.58	3	2	4	0.50		1.00		0.00	0.00	0.00	0.00	1.00
		03.27.07	0.25	0.50	1	0	4	0.00		0.00		0.25	0.00	0.00	0.00	0.00
		04.25.07	2.00	1.41	4	1	4	0.25		0.00		0.00	0.00	0.00	0.50	1.25

annual population density (A-6 to Ad) = 2.6 ind./core (=1000 ind./m^2)
annual maximum (A-6 to Ad) = 6.3 ind./core (=2400 ind./m^2)

annual population density (A-4 to Ad) = 1.8 ind./core (=700 ind./m^2)
annual maximum (A-4 to Ad) = 5.3 ind./core (=2000 ind./m^2)

TABLE AII-1
Continuation; *Cypridopsis vidua*.

species	site	sampling date	estimated abundance
Cypridopsis vidua[c)]	2 m[a)]	7.04.06	0
		25.4.06	0
		24.5.06	1-10
		19.6.06	11-100
		25.7.06	>101
		31.8.06	>101
		4.10.06	>101
		25.10.06	>101
		28.11.06	11-100
		9.1.07	11-100
		15.2.07	0
		12.3.07	11-100
		10.4.07	1-10
		1.5.07	11-100
	5 m[a)]	7.4.06	0
		25.4.06	0
		24.5.06	1-10
		19.6.06	11-100
		25.7.06	>101
		31.8.06	>101
		4.10.06	>101
		25.10.06	11-100
		28.11.06	1-10
		9.1.07	1-10
		15.2.07	1-10
		12.3.07	1-10
		10.4.07	0
		1.5.07	1-10

TABLE AII-1
Continuation; *Limnocythere inopinata* and *Limnocytherina sanctipatricii*.

species	site	sampling date	total abund.	std	max	min	nbr. of cores	female adultes	male adultes	female A-1	male A-2	A-2	A-3	A-4	A-5	A-6
Limnocythere inopinata	2 m[a)]	04.07.06	0					0		0		0				
		04.25.06	0					0		0		0				
		05.24.06	4					2		1		1				
		06.19.06	3					2		0		1				
		07.25.06	4					2		2		0				
		08.31.06	3					2		1		0				
		10.04.06	0					0		0		0				
		10.25.06	1					1		0		0				
		11.28.06	0					0		0		0				
		01.09.07	0					0		0		0				
		02.15.07	2					1		0		1				
		03.27.07	0					0		0		0				
		04.10.07	0					0		0		0				
		05.01.07	0					0		0		0				
	5 m[a)]	04.07.06	0					0		0		0				
		04.25.06	0					0		0		0				
		05.24.06	4					2		2		1				
		06.19.06	4					2		1		1				
		07.25.06	2					2		0		0				
		08.31.06	0					0		0		0				
		10.04.06	0					0		0		0				
		10.25.06	0					0		0		0				
		11.28.06	0					0		0		0				
		01.09.07	0					0		0		0				
		02.15.07	0					0		0		0				
		03.12.07	0					0		0		0				
		04.10.17	0					0		0		0				
		05.01.07	3					1		1		1				
	13 m	04.19.06	0	-	0	0	4	0		0		0				
		05.10.06	0	-	0	0	2	0		0		0				
		06.12.06	1.25	2.12	4	1	4	1		0.25		0				
		07.11.06	3	2.83	5	1	2	3		0		0				
		08.10.06	6.75	3.42	9	1	4	2.75		3		1				
		09.12.06	0.33	0.58	1	0	3	0.33		0		0				
		10.10.06	2	2.16	5	0	4	1.25		0.75		0				
		11.15.06	0	-	0	0	3	0		0		0				
		12.12.06	0.25	0.50	1	0	4	0.25		0		0				
		01.16.07	0.25	0.50	1	0	4	0.25		0		0				
		02.19.07	0	-	0	0	4	0		0		0				
		03.27.07	0	-	0	0	4	0		0		0				
		04.25.07	0	-	0	0	4	0		0		0				
		annual population density = 1.1 ind./core (=400 ind./m^2)														
		annual maximum = 6.8 ind./core (=2600 ind./m^2)														
Limnocytherina sanctipatricii	13 m	04.19.06	4.33	2.08	6	2	3	0.67	1.67	0.67	0.67	0.67	0			
		05.10.06	2	1.41	3	1	2	0.5	0	0	0.50	1	0			
		06.12.06	4.67	1.53	6	3	3	1	0.67	0	1.33	1.33	0.33			
		07.11.06	1.5	0.71	2	1	2	0.5	0	0.5	0.5	0	0			
		08.10.06	0	-	0	0	4	0	0	0	0	0	0			
		09.12.06	0	-	0	0	0	0	0	0	0	0	0			
		10.10.06	0	-	0	0	4	0	0	0	0	0	0			
		11.15.06	0	-	0	0	0	0	0	0	0	0	0			
		12.12.06	1	-	1	1	2	0	0	0	0.5	0	0.5			
		01.16.07	0.5	0.58	1	0	4	0	0	0	0	0.5	0			
		02.19.07	1.75	1.26	3	0	4	0	0.25	0.25	0.5	0.75	0			
		03.27.07	1.5	1.73	4	0	4	0.5	0	0.25	0	0.75	0			
		04.25.07	1	1.15	2	0	4	0.25	0.25	0.25	0	0.25	0			
		annual population density = 1.4 ind./core (=530 ind./m^2)														
		annual maximum = 4.7 ind./core (=1800 ind./m^2)														

TABLE AII-1
Continuation; *Cytherissa lacustris*.

species	site	sampling date	Total abundance	std	max	min	number of cores	Ad/1	Ad/2	Ad/3	A-1/1	A-1/2	A-1/3	A-2	A-3	A-4
Cytherissa lacustris[d)]	13 m	04.19.06	12.5	9.26	25	5	4	0.00	3.00	0.50	0.00	2.25	0.00	1.75	1.00	4.00
		05.10.06	18.67	12.22	32	8	3	2.00	3.67	0.33	0.33	0.67	0.00	2.67	3.33	5.67
		06.12.06	32.33	4.51	37	28	3	4.00	6.00	0.33	0.00	2.33	0.33	0.67	4.33	14.3
		07.11.06	50.5	37.48	77	24	2	8.00	4.00	0.00	0.00	2.50	0.00	1.50	10.0	24.5
		08.10.06	51.67	16.84	63	31	3	8.00	3.33	0.67	0.67	3.67	0.00	6.00	14.7	14.7
		09.12.06	47.67	29.14	75	17	3	6.67	4.67	0.00	0.00	2.67	0.00	16.7	11.3	5.67
		10.10.06	51	15.13	68	39	3	2.00	4.33	0.00	4.00	4.33	0.00	17.7	14.0	4.67
		11.15.06	26.33	15.04	42	12	3	1.00	4.33	1.00	1.00	6.00	0.00	8.00	3.67	1.33
		12.12.06	29.5	13.77	46	15	4	1.00	4.25	0.75	2.50	4.25	0.00	13.0	3.50	0.25
		01.16.07	36.25	9.95	44	22	4	1.50	6.50	1.75	2.75	14.5	0.25	6.00	2.25	0.75
		02.19.07	18.75	10.69	34	9	4	3.50	3.50	0.75	1.00	5.25	0.00	2.50	1.50	0.75
		03.27.07	20.5	12.61	39	12	4	0.50	4.75	0.00	0.75	4.75	0.00	1.50	2.25	6.00
		04.25.07	16.5	8.81	29	9	4	4.25	4.25	0.00	1.25	1.75	0.00	0.75	2.00	2.25
		annual population density = 31.7 ind./core (=12'000 ind./m^2)														
		annual maximum = 51.7 ind./core (=20'000 ind./m^2)														
	33 m	04.25.06	9.5	7	18	2	4	0.75	0.25	0.00	0.00	1.00	0.00	1.25	4.00	2.25
		06.19.06	8	3	11	5	3	0.67	0.67	0.33	0.00	1.33	0.00	1.67	2.33	1.00
		07.25.06	10.75	6.24	20	7	4	0.00	0.75	1.25	0.00	1.75	0.00	2.00	2.00	3.00
		08.21.06	19	2	21	17	3	0.33	0.33	0.33	0.00	2.67	0.67	2.33	4.00	8.33
		10.04.06	17.25	8.77	27	6	4	0.00	1.25	0.25	1.25	1.00	0.00	2.00	4.25	7.25
		10.25.06	22.75	9.43	31	8	4	0.25	1.25	0.00	1.50	2.75	0.00	1.25	7.00	8.75
		11.28.06	19.25	11.03	34	9	4	1.50	1.75	0.00	0.25	1.25	0.00	1.75	5.50	7.25
		01.09.07	25.5	5.26	33	21	4	1.00	2.00	0.25	0.50	2.00	0.00	5.25	9.00	5.50
		02.15.07	21.25	8.96	31	10	4	0.50	0.75	0.00	1.00	1.00	0.00	3.75	11.00	3.25
		03.12.07	23.25	10.05	36	12	4	1.75	1.50	0.00	0.00	1.00	0.00	5.50	8.75	4.75
		04.10.07	17	7.39	26	10	4	0.50	0.75	0.00	1.00	1.25	0.00	3.00	6.25	4.25
		05.01.07	16.25	6.4	23	8	4	0.50	2.25	0.00	0.25	0.50	0.00	3.25	5.25	4.25
		annual population density = 17.5 ind./core (=6600 ind./m^2)														
		annual maximum = 25.5 ind./core (=9700 ind./m^2)														
	70 m	04.19.06	14.5	9.68	29	9	4	1.00	3.25	1.25	0.75	1.25	0.25	1.25	1.25	0.75
		05.10.06	9	2.83	11	7	2	1.50	3.50	2.00	0.00	0.00	0.00	0.00	1.50	0.50
		06.12.06	26.5	10.61	34	19	2	2.00	7.00	1.00	0.00	4.50	0.00	5.00	3.00	4.00
		07.15.06	6.75	10.9	23	0	4	0.50	0.00	0.00	0.75	0.50	0.00	1.00	0.00	0.50
		08.23.06	44	50.91	80	8	2	4.00	11.50	4.00	2.00	8.00	0.00	9.00	2.00	3.50
		09.12.06	6.67	5.51	12	1	3	0.00	0.00	0.33	0.00	1.00	0.00	1.00	2.00	2.33
		10.10.06	27.75	30.43	73	7	4	0.00	0.75	0.50	0.75	2.00	0.00	0.25	4.25	4.50
		11.15.06	10.75	9.07	24	4	4	0.25	0.25	0.50	0.00	2.25	0.00	2.25	2.75	5.00
		12.12.06	24	11.37	41	17	4	0.50	0.75	1.50	0.25	1.00	0.00	3.50	8.00	6.75
		01.16.07	16.25	2.63	20	14	4	0.25	1.00	0.50	0.25	1.75	0.25	2.75	5.50	4.00
		02.19.07	20.25	15.13	42	9	4	0.50	1.50	0.75	0.75	2.00	0.00	4.00	6.00	3.00
		03.27.07	16.5	6.35	20	7	4	0.00	2.00	0.25	0.50	0.25	0.00	2.75	3.25	3.25
		04.25.07	31.5	14.11	49	15	4	0.50	1.75	0.75	1.75	3.50	0.00	4.25	5.75	4.50
		annual population density = 17.5 ind./core (=6600 ind./m^2)														
		annual maximum = 31.5 ind./core (=12'000 ind./m^2)														

a) at 2 and 5 m abundance figures reflect only relative abundance and is based on estimations
b) for *Cypria ophtalmica* forma *lacustris*, distinction was only done between adult and juveniles
c) for *Cypridopsis vidua*, only adults were taken in account, abundance were estimated.
d) for *Cytherissa lacustris*, adult and A-1 juveniles specimens were sub-grouped according to their "dirtiness". /1 stand for clean specimens, /2 for moderately coated specimens, /3 for highly coated specimens.

TABLE AII-2
Ostracod sediment penetration depth.

species	site	nbr. of cores	instars and gender	specimen abundance per sediment depth interval (cm) 0 - 0.5	0.5 - 1	1 - 1.5	1.5 - 2	2 - 3	3 - 4	4 - 5
Candona candida	13 m	13	Ad	2	1	0	0	0	0	0
			A-1	3	0	1	0	2	0	0
			A-2	3	7	4	2	0	0	0
			A-3	2	0	0	0	0	0	0
			A-4	1	1	0	0	0	0	0
	33 m	8	Ad	1	3	0	2	0	0	0
			A-1	0	0	1	0	0	0	0
			A-2	0	2	0	0	0	0	0
			A-3	0	1	0	0	0	0	0
			A-4	0	0	0	0	0	0	0
Candon neglecta	13 m	17	Ad F	10	9	2	0	0	0	0
			Ad M	3	3	5	0	0	0	0
			A-1	5	3	1	0	0	0	0
			A-1 F	3	1	1	0	0	0	0
			A-1 M	2	2	0	0	0	0	0
			A-2	17	36	19	7	3	0	0
			A-3	3	4	1	0	0	0	0
			A-4	2	0	0	0	0	0	0
	33 m	21	Ad F	2	3	8	4	3	0	0
			Ad M	0	7	1	1	1	0	0
			A-1 F	1	8	5	0	1	0	1
			A-1 M	1	4	4	0	1	0	0
			A-2	5	13	13	3	2	1	0
			A-3	1	8	4	1	0	0	0
			A-4	0	2	2	0	1	0	0
	70 m	20	Ad F	4	8	18	13	2	0	0
			Ad M	0	8	4	1	4	1	0
			A-1 F	1	4	7	5	0	0	0
			A-1 M	2	2	3	4	1	0	0
			A-2	0	6	2	4	8	2	0
			A-3	1	14	8	1	0	0	0
			A-4	3	9	5	2	5	0	0
Fabaeformiscandona caudata	13 m	26	Ad	4	4	3	0	0	1	0
			A-1	1	3	3	3	0	0	0
			A-2	26	35	17	7	0	0	0
			A-3	3	1	0	0	0	0	0
			A-4	2	1	0	0	0	0	0
Cypria ophtalmica	13 m	16	Ad	32	20	4	0	0	0	0
			Juv.	7	4	1	0	0	0	0
	33 m	6	Ad	3	4	1	1	0	0	0
	70 m	6	Ad	19	25	15	2	3	1	1
			Juv.	5	2	1	0	0	0	0
Herpetocypris reptans	13	20	Ad	4	10	3	2	2	0	0
			A-1	3	0	3	0	0	0	0
			A-2	2	1	1	0	0	0	0
			A-3	5	0	2	0	0	0	0
			A-4	6	1	0	0	0	0	0
			A-5	11	3	1	0	0	0	0
			A-6	12	2	0	0	0	0	0
Limnocytherina sanctipatricii	13	14	Ad F	6	0	1	0	0	0	0
			Ad M	1	1	0	0	0	0	0
			A-1	1	1	0	0	0	0	0
			A-2	3	1	1	0	0	0	0
			A-3	8	2	1	0	0	1	0
			A-4	2	0	0	0	0	0	0
Cytherissa lacustris	13	29	Ad	115	76	36	8	3	0	0
			A-1	91	73	18	2	4	0	0
			A-2	79	70	13	2	5	0	0
			A-3	98	46	8	5	1	1	0
			A-4	112	48	9	1	1	0	0
	33	21	Ad	16	10	4	1	2	0	0
			A-1	14	18	11	1	0	0	0
			A-2	12	20	9	0	2	0	0
			A-3	45	60	18	1	3	0	0
			A-4	54	40	9	0	1	0	0
	70	16	Ad	12	18	1	1	2	1	0
			A-1	9	20	5	3	0	0	0
			A-2	15	22	8	3	1	0	0
			A-3	19	39	14	7	1	0	0
			A-4	33	18	11	7	0	0	1

TABLE AII.3
Geochemical composition of *Candona candida*.

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
33	Ad	O	10.25.06	o331	5	1.4	-3.25	0.32	0.18	-7.33	0.29	0.15	2 w.	7.3	1 m.	-12.31	1.0361	3.75	5.5	1 m.	-	-	-	0.00478	0.00187	0.392
		Q	11.28.06	o274	6	6.0	-6.64	0.10	0.06	-8.18	0.14	0.08	1 m.	8.4	1 m.	-12.38	1.0353	3.12	8.9	1 m.	0.216	0.00396	0.0183	0.00486	0.00144	0.295
		S	01.09.07	o275	8	9.0	-6.54	0.06	0.06	-8.37	0.08	0.08	O.T.	-	Nov 07	-12.38	1.0351	-	9.7	-	-	-	-	-	-	-
		U	02.15.07	o276	6	6.5	-6.56	0.10	0.06	-8.15	0.07	0.08	O.T.	-	Nov 07	-12.38	1.0353	-	8.7	-	-	-	-	-	-	-
		W	03.12.07	o332	2	2.1	-6.35	0.17	0.18	-8.06	0.21	0.15	O.T.	-	Nov 07	-12.38	1.0354	-	8.3	-	-	-	-	-	-	-
		Y	04.10.07	o333	2	1.9	-6.47	0.14	0.18	-8.18	0.33	0.15	O.T.	-	Nov 07	-12.38	1.0353	-	8.9	-	-	-	-	-	-	-
		aa	05.01.07	o334	2	1.9	-7.08	0.26	0.18	-7.96	0.17	0.15	O.T.	-	Nov 07	-12.38	1.0355	-	7.9	-	-	-	-	-	-	-
	A-1	M	10.04.06	o343	4	1.5	-5.89	0.20	0.21	-7.91	0.49	0.14	2 m.	7.2	1 m.	-12.49	1.0357	3.24	7.2	1 m.	-	-	-	0.00486	0.00143	0.294
		O	10.25.06	o344	6	2.2	-6.00	0.18	0.21	-7.99	0.27	0.14	2 m.	7.4	1 m.	-12.31	1.0354	3.03	8.4	1 m.	-	-	-	0.00478	0.00144	0.301
	A-2	I	07.24.06	o406	6	1.1	-7.18	0.25	0.16	-7.69	0.45	0.14	3 w.	7.1	1 m.	-12.43	1.0359	3.28	6.5	sampl.	-	-	-	0.00482	0.00088	0.182
		K	08.31.06	o407	6	1.4	-6.33	0.27	0.16	-7.78	0.31	0.14	3 w.	7.0	1 m.	-12.33	1.0357	3.33	7.3	sampl.	-	-	-	0.00486	0.00090	0.185
		M	10.04.06	o408	8	1.9	-6.99	0.37	0.16	-7.77	0.30	0.14	3 w.	7.3	1 m.	-12.49	1.0358	3.21	6.6	sampl.	-	-	-	0.00478	0.00149	0.311
13	Ad	F	06.12.06	o335	2	2.3	-6.31	0.16	0.18	-8.25	0.20	0.15	O.T.	-	1 m.	-12.45	1.0353	-	8.9	1 m.	-	-	-	0.00398	0.00148	0.372
		P	11.15.06	o336	4	3.2	-3.76	0.12	0.18	-9.18	0.17	0.15	1 m.	14.0	1 m.	-12.38	1.0343	3.38	13.4	1 m.	-	-	-	0.00425	0.00192	0.453
		R	12.12.06	o337	2	1.8	-4.33	0.24	0.18	-8.20	0.28	0.15	1 m.	10.3	1 m.	-12.26	1.0351	3.41	9.5	1 m.	-	-	-	0.00495	0.00175	0.353
		T	01.16.07	o338	2	2.0	-6.09	0.22	0.18	-8.11	0.23	0.15	3 m.	7.8	1 m.	-12.21	1.0352	2.89	9.4	1 m.	-	-	-	0.00496	0.00156	0.314
		X	03.27.07	o339	2	2.1	-6.85	0.15	0.18	-8.43	0.17	0.15	O.T.	-	Jan 07	-12.21	1.0349	-	10.8	-	-	-	-	-	-	-
	A-1	P	11.15.06	o345	10	4.1	-5.39	0.16	0.10	-9.76	0.13	0.06	2 m.	14.4	1 m.	-12.38	1.0337	2.87	16.1	1 m.	0.227	0.00280	0.0123	0.00425	0.00161	0.379
		R	12.12.06	o346	4	1.8	-5.40	0.44	0.21	-9.17	0.34	0.14	2 m.	12.4	1 m.	-12.26	1.0341	2.90	14.0	1 m.	-	-	-	0.00495	0.00149	0.302
	A-2	F	06.12.06	o401	9	2.0	-5.39	0.28	0.05	-8.59	0.19	0.03	3 w.	10.3	1 m.	-12.45	1.0349	3.17	10.4	sampl.	-	-	-	0.00430	0.00163	0.380
		H	07.11.06	o402	14	3.8	-5.75	0.13	0.08	-9.01	0.19	0.06	3 w.	13.1	1 m.	-12.40	1.0344	3.36	12.6	sampl.	-	-	-	-	-	-
		J	08.10.06	o403	13	3.7	-5.17	0.15	0.08	-9.30	0.10	0.06	3 w.	14.4	1 m.	-12.39	1.0341	3.25	13.9	sampl.	-	-	-	0.00486	0.00152	0.313
		L	09.12.06	o404	11	3.0	-6.17	0.14	0.05	-9.22	0.25	0.03	3 w.	14.9	1 m.	-12.30	1.0341	3.43	14.0	sampl.	-	-	-	0.00392	0.00135	0.345
		N	10.10.06	o405	18	4.8	-5.68	0.08	0.08	-9.28	0.12	0.06	3 w.	14.6	1 m.	-12.28	1.0340	3.40	14.3	sampl.	-	-	-	0.00425	0.00146	0.344

TABLE AII.3
Geochemical composition of *Candona neglecta*.

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)		molar ratio			molar ratio		
Adult all values																										
70	Af	B	04.19.06	o288	2	2.7	-8.70	0.20	0.07	-6.98	0.25	0.07	2 m.	4.9	3 m.	-12.64	1.0368	3.82	4.0	1 m.	0.220	0.00334	0.0152	0.00367	0.00135	0.368
		D	05.16.06	o232	4	5.0	-7.91	0.09	0.10	-7.15	0.11	0.06	2 m.	4.8	3 m.	-12.64	1.0366	3.62	4.5	1 m.	0.220	0.00285	0.0130	0.00367	0.00131	0.358
		F	06.12.06	o233	7	7.8	-8.25	0.04	0.10	-7.57	0.08	0.06	2 m.	4.9	3 m.	-12.64	1.0362	3.20	5.9	1 m.	0.211	0.00294	0.0139	0.00371	0.00129	0.348
		H	07.11.06	o234	6	6.5	-8.21	0.08	0.10	-7.19	0.12	0.06	2 m.	5.0	3 m.	-12.64	1.0366	3.62	4.6	-	-	-	-	-	-	-
				o235	6	7.2	-8.42	0.10	0.10	-7.20	0.10	0.06	2 m.	5.0	3 m.	-12.64	1.0366	3.61	4.7	-	-	-	-	-	-	-
		J	08.10.06	o236	5	4.8	-8.06	0.11	0.10	-7.12	0.14	0.06	2 m.	5.2	3 m.	-12.41	1.0364	3.51	5.1	-	-	-	-	-	-	-
				o237	4	5.6	-8.18	0.10	0.10	-7.36	0.30	0.06	2 m.	5.2	3 m.	-12.41	1.0362	3.26	5.9	-	-	-	-	-	-	-
		L	09.12.06	o238	6	6.1	-7.58	0.09	0.10	-7.48	0.07	0.06	2 m.	5.4	3 m.	-12.58	1.0362	3.36	5.8	-	-	-	-	-	-	-
				o239	4	4.4	-8.08	0.09	0.10	-7.22	0.11	0.06	2 m.	5.4	3 m.	-12.58	1.0365	3.63	4.9	-	-	-	-	-	-	-
		N	10.10.06	o240	6	6.5	-7.74	0.10	0.10	-7.33	0.09	0.06	2 m.	5.5	3 m.	-12.33	1.0361	3.29	6.1	1 m.	0.215	0.00293	0.0136	0.00469	0.00129	0.276
				o241	6	6.5	-7.95	0.07	0.10	-7.30	0.12	0.06	2 m.	5.5	3 m.	-12.33	1.0362	3.31	6.0	1 m.	0.215	0.00375	0.0174	0.00469	0.00126	0.269
				o242	4	4.5	-8.21	0.16	0.10	-7.26	0.10	0.06	2 m.	5.5	3 m.	-12.33	1.0362	3.35	5.9	1 m.	0.215	0.00368	0.0171	0.00469	0.00130	0.277
				o243	4	5.0	-8.55	0.06	0.10	-7.47	0.13	0.06	2 m.	5.5	3 m.	-12.33	1.0360	3.14	6.6	1 m.	0.215	0.00384	0.0179	0.00469	0.00130	0.277
		P	11.15.06	o244	6	6.8	-7.92	0.11	0.10	-7.39	0.13	0.06	2 m.	5.6	3 m.	-12.39	1.0361	3.31	6.1	-	-	-	-	-	-	-
				o245	7	8.8	-8.24	0.06	0.10	-7.51	0.08	0.06	2 m.	5.6	3 m.	-12.39	1.0360	3.19	6.5	-	-	-	-	-	-	-
				o289	2	1.2	-6.97	0.37	0.07	-7.45	0.42	0.10	2 m.	5.6	3 m.	-12.39	1.0361	3.25	6.3	-	-	-	-	-	-	-
		R	11.15.06	o246	6	6.0	-8.26	0.09	0.10	-7.16	0.06	0.06	2 m.	5.7	3 m.	-12.45	1.0364	3.62	5.2	-	-	-	-	-	-	-
				o247	6	6.8	-8.10	0.06	0.10	-7.26	0.10	0.06	2 m.	5.7	3 m.	-12.45	1.0363	3.52	5.5	-	-	-	-	-	-	-
				o248	5	5.6	-8.90	0.14	0.10	-7.37	0.13	0.06	2 m.	5.7	3 m.	-12.45	1.0362	3.40	5.8	-	-	-	-	-	-	-
				o249	6	7.1	-8.05	0.06	0.10	-7.30	0.08	0.06	2 m.	5.7	3 m.	-12.45	1.0363	3.47	5.6	-	-	-	-	-	-	-
				o250	6	7.6	-8.40	0.07	0.10	-7.26	0.07	0.06	2 m.	5.7	3 m.	-12.45	1.0363	3.52	5.5	-	-	-	-	-	-	-
				o251	4	5.4	-8.65	0.09	0.10	-7.39	0.14	0.06	2 m.	5.7	3 m.	-12.45	1.0362	3.39	5.9	-	-	-	-	-	-	-
		T	01.16.07	o252	6	6.9	-7.79	0.08	0.10	-7.29	0.09	0.06	2 m.	5.7	3 m.	-12.34	1.0362	3.37	5.9	-	-	-	-	-	-	-
				o253	6	7.3	-8.30	0.08	0.10	-7.32	0.09	0.06	2 m.	5.7	3 m.	-12.34	1.0362	3.34	6.0	-	-	-	-	-	-	-
				o254	6	7.3	-8.44	0.04	0.10	-7.39	0.10	0.06	2 m.	5.7	3 m.	-12.34	1.0361	3.26	6.3	-	-	-	-	-	-	-
				o255	6	7.7	-8.49	0.12	0.10	-7.34	0.09	0.06	2 m.	5.7	3 m.	-12.34	1.0361	3.32	6.1	-	-	-	-	-	-	-
		V	02.20.07	o256	6	6.4	-8.45	0.08	0.10	-7.34	0.09	0.06	2 m.	5.7	3 m.	-12.29	1.0361	3.27	6.3	-	-	-	-	-	-	-
				o257	6	6.9	-8.64	0.11	0.10	-7.44	0.10	0.06	2 m.	5.7	3 m.	-12.29	1.0360	3.17	6.6	-	-	-	-	-	-	-
		X	03.27.07	o290	2	3.3	-8.84	0.07	0.07	-7.70	0.11	0.07	2 m.	5.8	3 m.	-12.28	1.0357	2.92	7.5	1 m.	0.213	0.00356	0.0167	0.00355	0.00127	0.358
				o258	6	7.1	-8.25	0.08	0.10	-7.29	0.06	0.06	2 m.	5.8	3 m.	-12.28	1.0361	3.35	6.1	1 m.	0.213	0.00263	0.0123	0.00355	0.00126	0.356
				o259	6	7.4	-8.71	0.08	0.10	-7.37	0.10	0.06	2 m.	5.8	3 m.	-12.28	1.0360	3.25	6.4	1 m.	0.213	0.00291	0.0136	0.00355	0.00134	0.376
		Z	04.25.07	o291	2	1.4	-6.63	0.28	0.07	-7.36	0.35	0.10	2 m.	6.1	3 m.	-12.21	1.0360	3.25	6.6	1 m.	-	-	-	0.00361	0.00160	0.444
	Am	B	04.19.06	o159	2	3.4	-8.23	0.10	0.08	-7.22	0.19	0.11	3 m.	4.79	2 m.	-12.64	1.0366	3.54	4.7	1 m.	-	-	-	0.00367	0.00130	0.353
		F	06.12.06	o160	4	6.0	-8.02	0.08	0.07	-7.02	0.17	0.08	3 m.	4.90	2 m.	-12.64	1.0368	3.77	4.1	1 m.	-	-	-	0.00371	0.00119	0.322
				o161	2	2.5	-7.44	0.21	0.12	-6.97	0.21	0.09	3 m.	4.90	2 m.	-12.64	1.0368	3.82	3.9	1 m.	-	-	-	0.00371	0.00134	0.361
		H	07.11.06	o162	4	4.6	-7.57	0.13	0.08	-7.09	0.13	0.11	3 m.	5.11	2 m.	-12.41	1.0365	3.52	5.0	1 m.	-	-	-	0.00381	0.00129	0.340
				o163	2	2.4	-8.00	0.21	0.12	-7.01	0.11	0.09	3 m.	5.11	2 m.	-12.41	1.0366	3.60	4.8	1 m.	-	-	-	0.00381	0.00142	0.374
		J	08.10.06	o164	4	5.1	-7.10	0.10	0.08	-7.15	0.14	0.08	3 m.	5.30	2 m.	-12.58	1.0366	3.68	4.7	1 m.	-	-	-	0.00374	0.00137	0.367
				o165	4	6.3	-8.33	0.09	0.07	-7.28	0.13	0.08	3 m.	5.30	2 m.	-12.58	1.0365	3.55	5.1	1 m.	0.222	0.00411	0.0186	0.00374	0.00123	0.328
				o166	4	5.4	-7.78	0.06	0.08	-7.19	0.13	0.08	3 m.	5.30	2 m.	-12.58	1.0365	3.63	4.8	1 m.	-	-	-	0.00374	0.00123	0.329
				o167	5	6.7	-7.76	0.06	0.07	-7.21	0.10	0.08	3 m.	5.30	2 m.	-12.58	1.0365	3.61	4.9	1 m.	-	-	-	0.00374	0.00131	0.352
		L	09.12.06	o168	6	5.9	-7.38	0.11	0.08	-7.44	0.12	0.08	3 m.	5.49	2 m.	-12.33	1.0360	3.16	6.5	1 m.	0.214	0.00436	0.0203	0.00424	0.00133	0.314
				o169	4	5.7	-7.52	0.11	0.08	-7.26	0.12	0.08	3 m.	5.49	2 m.	-12.33	1.0362	3.34	5.9	1 m.	-	-	-	0.00424	0.00128	0.302
		N	10.10.06	o170	4	6.0	-7.79	0.13	0.08	-7.63	0.15	0.08	3 m.	5.60	2 m.	-12.39	1.0359	3.05	6.9	1 m.	0.215	0.00406	0.0189	0.00469	0.00125	0.267
				o171	4	4.4	-6.74	0.11	0.08	-7.21	0.17	0.11	3 m.	5.60	2 m.	-12.39	1.0363	3.48	5.5	1 m.	-	-	-	0.00469	0.00137	0.291
				o172	4	5.7	-6.65	0.09	0.08	-7.30	0.17	0.08	3 m.	5.60	2 m.	-12.39	1.0362	3.39	5.8	1 m.	-	-	-	0.00469	0.00131	0.278
				o173	4	4.7	-7.06	0.11	0.08	-7.35	0.11	0.11	3 m.	5.60	2 m.	-12.39	1.0362	3.34	6.0	1 m.	-	-	-	0.00469	0.00129	0.274
		P	11.15.06	o174	4	4.9	-7.70	0.13	0.08	-7.34	0.36	0.08	3 m.	5.70	2 m.	-12.45	1.0362	3.43	5.8	1 m.	-	-	-	0.00365	0.00124	0.340
		R	12.12.06	o175	4	6.1	-7.55	0.07	0.07	-7.28	0.16	0.08	3 m.	5.71	2 m.	-12.34	1.0362	3.39	5.9	1 m.	-	-	-	0.00376	0.00120	0.320
				o176	4	5.5	-7.77	0.53	0.08	-7.50	0.62	0.08	3 m.	5.71	2 m.	-12.34	1.0360	3.16	6.6	1 m.	0.213	0.00529	0.0249	0.00376	0.00126	0.335
				o177	2	3.1	-7.79	0.17	0.08	-7.35	0.16	0.11	3 m.	5.71	2 m.	-12.34	1.0361	3.32	6.1	-	-	-	-	-	-	-
				o178	4	5.5	-8.22	0.09	0.08	-7.33	0.11	0.08	3 m.	5.71	2 m.	-12.34	1.0361	3.34	6.1	-	-	-	-	-	-	-
				o179	4	5.6	-7.51	0.06	0.08	-7.45	0.15	0.08	3 m.	5.71	2 m.	-12.34	1.0360	3.22	6.5	-	-	-	-	-	-	-

Adult all values																								
70	Am	T	01.16.07	o180	4	5.1	-7.74	0.11	0.08	-7.33	0.22	0.08	3 m.	5.67	2 m.	-12.29	1.0361	3.28	6.2	-	-	-	-	-	-	-
				o181	2	2.9	-8.00	0.18	0.12	-7.39	0.23	0.09	3 m.	5.67	2 m.	-12.29	1.0360	3.22	6.4	-	-	-	-	-	-	-
		V	02.20.07	o182	2	2.5	-7.28	0.15	0.12	-6.99	0.15	0.09	3 m.	5.66	2 m.	-12.28	1.0364	3.61	5.2	-	-	-	-	-	-	-
				o183	4	5.0	-8.19	0.09	0.08	-7.06	0.07	0.08	3 m.	5.66	2 m.	-12.28	1.0364	3.54	5.4	-	-	-	-	-	-	-
		Z	04.25.07	o184	4	4.4	-7.70	0.10	0.08	-7.26	0.13	0.11	3 m.	6.22	2 m.	-12.33	1.0362	3.52	5.9	-	-	-	-	-	-	-
Adult monthly averages																								
	Af	B	04.19.06				-8.70			-6.98			2 m.	4.93	3 m.	-12.64	1.0368	3.77	4.0	1 m.	0.220	0.00334	0.0152	0.00367	0.00135	0.368
		D	05.16.06				-7.91			-7.15			2 m.	4.84	3 m.	-12.64	1.0366	3.65	4.5	1 m.	0.220	0.00285	0.0130	0.00367	0.001314	0.358
		F	06.12.06				-8.25			-7.57			2 m.	4.87	3 m.	-12.64	1.0362	3.26	5.9	1 m.	0.211	0.00294	0.0139	0.00371	0.001293	0.348
		H	07.11.06				-8.31			-7.19			2 m.	5.00	3 m.	-12.64	1.0366	3.69	4.7	-	-	-	-	-	-	-
		J	08.10.06				-8.12			-7.24			2 m.	5.20	3 m.	-12.41	1.0363	3.45	5.5	-	-	-	-	-	-	-
		L	09.12.06				-7.83			-7.35			2 m.	5.39	3 m.	-12.58	1.0364	3.55	5.3	-	-	-	-	-	-	-
		N	10.10.06				-8.11			-7.34			2 m.	5.53	3 m.	-12.33	1.0361	3.31	6.1	1 m.	0.215	0.00355	0.0165	0.00469	0.001288	0.275
		P	11.15.06				-7.71			-7.45			2 m.	5.64	3 m.	-12.39	1.0361	3.28	6.3	-	-	-	-	-	-	-
		R	11.15.06				-8.39			-7.29			2 m.	5.69	3 m.	-12.45	1.0363	3.50	5.6	-	-	-	-	-	-	-
		T	01.16.07				-8.26			-7.33			2 m.	5.67	3 m.	-12.34	1.0361	3.30	6.1	-	-	-	-	-	-	-
		V	02.20.07				-8.54			-7.39			2 m.	5.69	3 m.	-12.29	1.0360	3.24	6.4	-	-	-	-	-	-	-
		X	03.27.07				-8.60			-7.45			2 m.	5.82	3 m.	-12.28	1.0360	3.29	6.7	1 m.	0.213	0.00303	0.0142	0.00355	0.001292	0.363
		Z	04.25.07				-6.63			-7.36			2 m.	6.05	3 m.	-12.21	1.0360	3.38	6.6	1 m.	-	-	-	0.00361	0.001605	0.444
	Am	B	04.19.06				-8.23			-7.22			3 m.	4.79	2 m.	-12.64	1.0366	3.54	4.7	1 m.	-	-	-	0.00367	0.001296	0.353
		F	06.12.06				-7.73			-7.00			3 m.	4.90	2 m.	-12.64	1.0368	3.79	4.0	1 m.	-	-	-	0.00371	0.001266	0.341
		H	07.11.06				-7.79			-7.05			3 m.	5.11	2 m.	-12.41	1.0365	3.56	4.9	1 m.	-	-	-	0.00381	0.001359	0.357
		J	08.10.06				-7.74			-7.21			3 m.	5.30	2 m.	-12.58	1.0365	3.62	4.9	1 m.	0.222	0.00411	0.0186	0.00374	0.001285	0.344
		L	09.12.06				-7.45			-7.35			3 m.	5.49	2 m.	-12.33	1.0361	3.25	6.2	1 m.	0.214	0.00436	0.0203	0.00424	0.001305	0.308
		N	10.10.06				-7.06			-7.37			3 m.	5.60	2 m.	-12.39	1.0362	3.32	6.1	1 m.	0.215	0.00406	0.0189	0.00469	0.001304	0.278
		P	11.15.06				-7.70			-7.34			3 m.	5.70	2 m.	-12.45	1.0362	3.43	5.8	1 m.	-	-	-	0.00365	0.001241	0.340
		R	12.12.06				-7.77			-7.38			3 m.	5.71	2 m.	-12.34	1.0361	3.28	6.2	1 m.	0.213	0.00529	0.0249	0.00376	0.001233	0.328
		T	01.16.07				-7.87			-7.36			3 m.	5.67	2 m.	-12.29	1.0361	3.25	6.3	-	-	-	-	-	-	-
		V	02.20.07				-7.74			-7.03			3 m.	5.66	2 m.	-12.28	1.0364	3.57	5.3	-	-	-	-	-	-	-
		Z	04.25.07				-7.70			-7.26			3 m.	6.22	2 m.	-12.33	1.0362	3.52	5.9	-	-	-	-	-	-	-
Juveniles all values																								
	A-1f	B	04.19.06	o300	5	2.0	-5.89	0.20	0.07	-6.69	0.23	0.10	2 m.	4.72	3 m.	-12.64	1.0371	4.07	3.0	1 m.	-	-	-	0.00367	0.001457	0.397
		J	08.10.06	o302	8	3.0	-7.77	0.10	0.13	-7.27	0.11	0.09	2 m.	5.40	3 m.	-12.41	1.0363	3.40	5.6	-	-	-	-	-	-	-
		L	09.12.06	o301	10	4.0	-7.45	0.14	0.07	-7.64	0.13	0.07	2 m.	5.56	3 m.	-12.58	1.0361	3.23	6.3	-	-	-	-	-	-	-
		N	10.10.06	o282	13	5.5	-7.59	0.05	0.06	-7.35	0.13	0.08	2 m.	5.66	3 m.	-12.33	1.0361	3.30	6.2	-	-	-	-	-	-	-
		R	12.12.06	o303	4	1.4	-7.01	0.23	0.18	-7.26	0.37	0.11	2 m.	5.73	3 m.	-12.45	1.0363	3.53	5.5	-	-	-	-	-	-	-
		T	01.16.07	o304	6	2.3	-7.61	0.10	0.18	-7.18	0.22	0.11	2 m.	5.63	3 m.	-12.34	1.0363	3.47	5.6	1 m.	-	-	-	0.00375	0.00148	0.394
		V	02.20.07	o305	6	2.6	-7.65	0.21	0.13	-6.97	0.94	0.09	2 m.	5.66	3 m.	-12.29	1.0365	3.64	5.1	-	-	-	-	-	-	-
		Z	04.25.07	o306	4	1.6	-7.19	0.14	0.18	-7.38	0.19	0.11	2 m.	6.43	3 m.	-12.21	1.0360	3.32	6.7	1 m.	-	-	-	0.00361	0.001353	0.375
	A-1	X	03.27.07	o328	5	2.4	-7.96	0.15	0.04	-7.54	0.16	0.08	2 m.	6.05	3 m.	-12.28	1.0359	3.14	7.0	1 m.	-	-	-	0.00355	0.001362	0.383
	A-1m	A	04.07.06	o312	4	1.8	-7.47	0.19	0.18	-6.85	0.29	0.11	2 m.	4.73	3 m.	-12.64	1.0370	3.91	3.5	-	-	-	-	-	0.001164	-
		D	05.16.06	o313	4	1.7	-6.75	0.09	0.18	-7.17	0.20	0.11	2 m.	4.82	3 m.	-12.64	1.0366	3.60	4.6	1 m.	-	-	-	0.00367	0.001052	0.286
		H	07.11.06	o314	6	2.5	-8.14	0.16	0.18	-7.22	0.35	0.11	2 m.	5.22	3 m.	-12.64	1.0366	3.64	4.7	-	-	-	-	-	-	-
		J	08.10.06	o315	8	3.6	-8.01	0.08	0.13	-7.26	0.17	0.09	2 m.	5.40	3 m.	-12.41	1.0363	3.41	5.6	-	-	-	-	-	-	-
		L	09.12.06	o318	4	2.0	-7.07	0.15	0.17	-7.38	0.20	0.12	2 m.	5.56	3 m.	-12.58	1.0364	3.50	5.4	1 m.	-	-	-	0.00424	0.001717	0.405
		T	01.16.07	o319	4	2.0	-8.55	0.30	0.17	-7.57	0.34	0.12	2 m.	5.63	3 m.	-12.34	1.0359	3.07	6.9	-	-	-	-	-	-	-
		Z	04.25.07	o320	6	2.9	-8.26	0.20	0.04	-7.47	0.23	0.08	2 m.	6.43	3 m.	-12.21	1.0359	3.23	6.9	1 m.	-	-	-	0.00361	0.001578	0.437

Table AII.4. *Candona neglecta*

Juveniles all values																								
70	A-2	D	05.16.06	o391	4	1.0	-7.33	0.52	0.12	-6.98	0.26	0.07	2 m.	4.82	3 m.	-12.64	1.0368	3.79	4.0	1 m.	-	-	-	0.00367	0.001261	0.343
		F	06.12.06	o392	6	1.5	-7.72	0.30	0.12	-7.28	0.25	0.07	2 m.	5.01	3 m.	-12.64	1.0365	3.53	4.9	1 m.	-	-	-	0.00371	0.001296	0.349
		H	07.11.06	o393	14	3.0	-7.79	0.10	0.12	-7.33	0.23	0.07	2 m.	5.22	3 m.	-12.64	1.0365	3.53	5.1	1 m.	-	-	-	0.00381	0.001501	0.394
		J	08.10.06	o394	27	6.7	-8.04	0.08	0.08	-7.45	0.11	0.07	2 m.	5.40	3 m.	-12.41	1.0361	3.21	6.2	-	-	-	-	-	-	-
		L	09.12.06	o395	12	3.2	-7.81	0.13	0.12	-7.66	0.21	0.07	2 m.	5.56	3 m.	-12.58	1.0361	3.22	6.3	-	-	-	-	-	-	-
		N	10.10.06	o396	8	2.0	-7.84	0.21	0.12	-7.36	0.26	0.07	2 m.	5.66	3 m.	-12.33	1.0361	3.28	6.2	-	-	-	-	-	-	-
		R	12.12.06	o397	8	2.1	-7.55	0.16	0.12	-7.22	0.23	0.07	2 m.	5.73	3 m.	-12.45	1.0364	3.57	5.3	-	-	-	-	-	-	-
		V	02.20.07	o398	14	3.4	-7.60	0.10	0.12	-7.20	0.17	0.07	2 m.	5.66	3 m.	-12.29	1.0362	3.40	5.8	-	-	-	-	-	-	-
		X	03.27.07	o399	8	1.8	-7.79	0.21	0.12	-7.24	0.16	0.07	2 m.	6.05	3 m.	-12.28	1.0362	3.45	6.0	1 m.	-	-	-	0.00355	0.001404	0.395
		Z	04.25.07	o400	13	3.3	-7.60	0.13	0.12	-7.33	0.16	0.07	2 m.	6.43	3 m.	-12.21	1.0360	3.38	6.5	1 m.	-	-	-	0.00361	0.001475	0.408
Adult all values																								
33	Af	C	04.25.06	o215	4	4.4	-8.46	0.17	0.09	-7.13	0.12	0.07	4 m.	5.15	1 m.	-12.51	1.0365	3.58	4.9	2 m.	-	-	-	0.00483	0.00122	0.253
		E	05.24.06	o216	6	7.5	-8.70	0.08	0.09	-7.37	0.19	0.07	4 m.	5.31	1 m.	-12.46	1.0362	3.32	5.8	2 m.	-	-	-	0.00483	0.00120	0.247
		G	06.19.06	o217	6	5.8	-8.33	0.09	0.09	-7.35	0.14	0.07	4 m.	5.84	1 m.	-12.41	1.0362	3.42	5.9	-	-	-	-	-	-	-
				o218	8	9.2	-8.71	0.08	0.09	-7.11	0.06	0.07	4 m.	5.84	1 m.	-12.41	1.0365	3.67	5.1	-	-	-	-	-	-	-
		I	07.24.06	o219	4	4.7	-7.67	0.13	0.09	-7.33	0.10	0.07	4 m.	6.44	1 m.	-12.43	1.0362	3.60	5.8	-	-	-	-	-	-	-
				o220	6	7.2	-8.55	0.06	0.09	-7.13	0.12	0.07	4 m.	6.44	1 m.	-12.43	1.0365	3.81	5.1	-	-	-	-	-	-	-
				o292*	5	2.3	-6.64	0.14	0.07	-7.22	0.26	0.07			1 m.											
		K	08.31.06	o221	6	5.5	-7.46	0.08	0.09	-7.46	0.12	0.07	4 m.	6.86	1 m.	-12.33	1.0360	3.46	6.5	-	-	-	-	-	-	-
				o222	6	7.1	-7.79	0.09	0.09	-7.45	0.11	0.07	4 m.	6.86	1 m.	-12.33	1.0360	3.47	6.5	-	-	-	-	-	-	-
		M	10.04.06	o223	6	7.7	-8.76	0.07	0.09	-7.72	0.11	0.07	4 m.	7.11	1 m.	-12.49	1.0359	3.41	6.9	-	-	-	-	-	-	-
				o224	6	7.9	-8.06	0.05	0.09	-7.65	0.12	0.07	4 m.	7.11	1 m.	-12.49	1.0360	3.49	6.6	-	-	-	-	-	-	-
		O	10.25.06	o225	6	6.2	-8.29	0.09	0.09	-7.54	0.12	0.07	4 m.	7.21	1 m.	-12.31	1.0359	3.44	6.9	-	-	-	-	-	-	-
				o226	7	8.8	-8.17	0.09	0.09	-7.51	0.10	0.07	4 m.	7.21	1 m.	-12.31	1.0359	3.48	6.8	-	-	-	-	-	-	-
		Q	11.28.06	o293*	2	1.4	-8.19	0.18	0.07	-7.68	0.41	0.10			1 m.											
				o227	2	5.1	-8.07	0.16	0.09	-7.67	0.14	0.07	4 m.	7.58	1 m.	-12.38	1.0358	3.47	7.1	2 m.	-	-	-	0.00478	0.00118	0.246
		S	01.09.07	o228	6	5.6	-8.17	0.09	0.09	-7.58	0.18	0.07	4 m.	7.88	1 m.	-12.31	1.0359	3.56	7.0	2 m.	-	-	-	0.00486	0.00119	0.245
		W	03.12.07	o229	6	6.0	-8.70	0.07	0.09	-7.23	0.08	0.07	4 m.	7.13	1 m.	-12.21	1.0361	3.64	6.2	-	-	-	-	-	-	-
		Y	04.10.07	o230	4	4.2	-8.80	0.13	0.09	-7.15	0.21	0.07	4 m.	6.80	1 m.	-12.16	1.0361	3.59	6.1	-	-	-	-	-	-	-
		aa	05.01.07	o231	6	5.7	-8.68	0.11	0.09	-7.27	0.11	0.07	4 m.	6.57	1 m.	-12.26	1.0361	3.51	6.2	2 m.	-	-	-	0.00486	0.00116	0.239
	Am	A	04.07.06	o148	4	5.7	-8.41	0.13	0.07	-7.12	0.20	0.10	3 m.	4.99	2 m.	-12.51	1.0365	3.55	4.8	1 m.	-	-	-	0.00483	0.00123	0.255
		C	04.25.06	o149	2	2.6	-8.97	0.17	0.13	-7.12	0.12	0.19	3 m.	5.10	2 m.	-12.51	1.0365	3.58	4.8	1 m.	-	-	-	0.00483	0.00131	0.270
				o150	4	2.5	-7.00	0.18	0.13	-7.14	0.20	0.19	3 m.	5.10	2 m.	-12.51	1.0365	3.56	4.9	1 m.	-	-	-	0.00483	0.00128	0.264
				o151	2	2.8	-8.13	0.11	0.13	-7.11	0.16	0.19	3 m.	5.10	2 m.	-12.51	1.0366	3.59	4.8	1 m.	-	-	-	0.00483	0.00119	0.247
		G	06.19.06	o152	2	2.9	-7.50	0.13	0.13	-7.69	0.16	0.19	3 m.	6.17	2 m.	-12.46	1.0359	3.19	6.9	1 m.	-	-	-	0.00451	0.00118	0.262
		I	07.25.06	o153	2	2.4	-7.80	0.18	0.13	-7.41	0.24	0.19	3 m.	6.75	2 m.	-12.41	1.0361	3.57	6.1	1 m.	-	-	-	0.00498	0.00121	0.243
		W	03.12.07	o154	4	5.3	-8.24	0.05	0.16	-7.66	0.10	0.14	3 m.	6.81	2 m.	-12.31	1.0358	3.23	7.2	1 m.	-	-	-	0.00484	0.00124	0.257
		Y	04.10.07	o155	2	1.5	-5.84	0.25	0.22	-7.29	0.39	0.25	3 m.	6.45	2 m.	-12.21	1.0361	3.42	6.4	1 m.	-	-	-	0.00486	0.00153	0.315
				o156	4	4.9	-7.91	0.12	0.16	-7.33	0.11	0.14	3 m.	6.45	2 m.	-12.21	1.0360	3.37	6.5	1 m.	-	-	-	0.00486	0.00120	0.246
		aa	05.01.07	o157	4	4.5	-7.75	0.13	0.16	-7.32	0.24	0.14	3 m.	6.57	2 m.	-12.16	1.0360	3.37	6.6	1 m.	-	-	-	0.00497	0.00127	0.255
				o158	4	5.1	-8.46	0.08	0.16	-7.51	0.12	0.14	3 m.	6.57	2 m.	-12.16	1.0358	3.17	7.3	1 m.	-	-	-	0.00497	0.00130	0.261
Adult monthly averages																								
	Af	C	04.25.06				-8.46			-7.13			4 m.	5.15	1 m.	-12.51	1.0365	3.68	4.9	2 m.	-	-	-	0.00483	0.001225	0.253
		E	05.24.06				-8.70			-7.37			4 m.	5.31	1 m.	-12.46	1.0362	3.48	5.8	2 m.	-	-	-	0.00483	0.001195	0.247
		G	06.19.06				-8.52			-7.23			4 m.	5.84	1 m.	-12.41	1.0363	3.85	5.5	-	-	-	-	-	-	-
		I	07.24.06				-7.62			-7.23			4 m.	6.44	1 m.	-12.43	1.0364	3.84	5.4	-	-	-	-	-	-	-
		K	08.31.06				-7.63			-7.46			4 m.	6.86	1 m.	-12.33	1.0360	3.50	6.5	-	-	-	-	-	-	-
		M	10.04.06				-8.41			-7.69			4 m.	7.11	1 m.	-12.49	1.0359	3.49	6.8	-	-	-	-	-	-	-
		O	10.25.06				-8.23			-7.52			4 m.	7.21	1 m.	-12.31	1.0359	3.55	6.8	-	-	-	-	-	-	-
		Q	11.28.06				-8.13			-7.67			4 m.	7.58	1 m.	-12.38	1.0358	3.65	7.1	2 m.	-	-	-	0.00478	0.001178	0.246
		S	01.09.07				-8.17			-7.58			4 m.	7.88	1 m.	-12.31	1.0359	3.55	7.0	2 m.	-	-	-	0.00486	0.001191	0.245
		W	03.12.07				-8.70			-7.23			4 m.	7.13	1 m.	-12.21	1.0361	3.43	6.2	-	-	-	-	-	-	-
		Y	04.10.07				-8.80			-7.15			4 m.	6.80	1 m.	-12.16	1.0361	3.58	6.1	-	-	-	-	-	-	-
		aa	05.01.07				-8.68			-7.27			4 m.	6.57	1 m.	-12.26	1.0361	3.62	6.2	2 m.	-	-	-	0.00486	0.001161	0.239

Adult monthly averages																									
33	Am	A	04.07.06				-8.41			-7.12			3 m.	4.99	2 m.	-12.51	1.0365	3.55	4.8	1 m.	-	-	-	0.00483	0.001234	0.255
		C	04.25.06				-8.03			-7.13			3 m.	5.10	2 m.	-12.51	1.0365	3.58	4.8	1 m.	-	-	-	0.00483	0.001259	0.261
		G	06.19.06				-7.50			-7.69			3 m.	6.17	2 m.	-12.46	1.0359	3.19	6.9	1 m.	-	-	-	0.00451	0.001181	0.262
		I	07.25.06				-7.80			-7.41			3 m.	6.75	2 m.	-12.41	1.0361	3.57	6.1	1 m.	-	-	-	0.00498	0.001214	0.243
		W	03.12.07				-8.24			-7.66			3 m.	6.81	2 m.	-12.31	1.0358	3.23	7.2	1 m.	-	-	-	0.00484	0.001245	0.257
		Y	04.10.07				-6.87			-7.31			3 m.	6.45	2 m.	-12.21	1.0360	3.40	6.4	1 m.	-	-	-	0.00486	0.001363	0.281
		aa	05.01.07				-8.10			-7.41			3 m.	6.57	2 m.	-12.16	1.0359	3.27	6.9	1 m.	-	-	-	0.00497	0.001282	0.258
Juveniles all values																									
	A-1f	C	04.25.06	o316	6	2.6	-8.37	0.17	0.13	-7.58	0.27	0.09	3 w.	5.93	1 m.	-12.51	1.0361	3.30	6.3	sampl.	-	-	-	0.00465	0.00107	0.230
		E	05.24.06	o307	4	1.5	-8.12	0.21	0.18	-7.59	0.28	0.11	3 w.	5.93	1 m.	-12.46	1.0360	3.25	6.5	-	-	-	-	-	-	-
		I	07.24.06	o308	4	1.4	-7.93	0.34	0.18	-7.89	0.43	0.11	3 w.	7.09	1 m.	-12.43	1.0357	3.18	7.6	-	-	-	-	-	-	-
		S	01.09.07	o309	6	2.4	-7.84	0.12	0.18	-7.89	0.25	0.11	3 w.	7.56	1 m.	-12.31	1.0355	3.17	8.0	sampl.	-	-	-	0.00478	0.001339	0.280
		W	03.12.07	o283	21	8.2	-7.81	0.08	0.06	-7.33	0.05	0.08	3 w.	6.26	1 m.	-12.21	1.0360	3.34	6.5	-	-	-	-	-	-	-
		Y	04.10.07	o310	10	3.6	-8.26	0.13	0.13	-7.45	0.19	0.09	3 w.	6.81	1 m.	-12.16	1.0358	3.29	7.1	sampl.	-	-	-	0.00497	0.001257	0.253
		aa	05.01.07	o284	17	6.6	-8.01	0.10	0.06	-7.35	0.05	0.08	3 w.	7.01	1 m.	-12.26	1.0360	3.53	6.4	-	-	-	-	-	-	-
	A-1	A	04.07.06	o329	4	2.0	-8.58	0.12	0.17	-7.29	0.20	0.12	3 w.	4.91	1 m.	-12.51	1.0364	3.36	5.4	sampl.	-	-	-	0.00483	0.001352	0.280
		U	02.15.07	o330	4	1.4	-6.67	0.35	0.17	-6.83	0.64	0.12	3 w.	6.15	1 m.	-12.31	1.0366	3.92	4.5	-	-	-	-	-	-	-
	A-1m	C	04.25.06	o321	8	3.5	-7.96	0.16	0.04	-7.46	0.12	0.08	3 w.	5.93	1 m.	-12.51	1.0362	3.42	6.0	sampl.	-	-	-	0.00465	0.001492	0.321
		G	06.19.06	o322	4	1.7	-6.65	0.18	0.17	-7.89	0.24	0.12	3 w.	7.63	1 m.	-12.41	1.0356	3.28	7.7	sampl.	-	-	-	0.00498	0.001455	0.292
		W	03.12.07	o323	4	1.9	-7.59	0.33	0.17	-7.27	0.24	0.12	3 w.	6.26	1 m.	-12.21	1.0361	3.39	6.3	-	-	-	-	-	-	-
		Y	04.10.07	o285	14	6.1	-8.55	0.11	0.06	-7.43	0.19	0.08	3 w.	6.81	1 m.	-12.16	1.0359	3.31	7.0	sampl.	-	-	-	0.00497	0.001327	0.267
		aa	05.01.07	o324	4	1.9	-8.88	0.28	0.17	-7.42	0.29	0.12	3 w.	7.01	1 m.	-12.26	1.0360	3.46	6.7	-	-	-	-	-	-	-
	A-2	A	04.07.06	o380	6	1.1	-7.37	0.23	0.12	-6.97	0.34	0.07	1 m.	4.87	3 m.	-12.51	1.0367	3.68	4.3	1 m.	-	-	-	0.00483	0.001244	0.257
		C	04.25.06	o381	12	2.7	-7.94	0.17	0.12	-7.46	0.25	0.07	1 m.	5.58	3 m.	-12.51	1.0362	3.35	5.9	1 m.	-	-	-	0.00483	0.001235	0.255
		O	10.25.06	o384	6	0.5	-6.69	0.51	0.12	-7.60	0.44	0.07	1 m.	7.60	3 m.	-12.33	1.0359	3.49	7.0	-	-	-	-	-	-	-
		Q	11.28.06	o385	13	2.4	-7.36	0.14	0.12	-8.21	0.16	0.07	1 m.	8.36	3 m.	-12.49	1.0354	3.20	8.5	1 m.	0.216	0.00489	0.0226	0.00486	0.001317	0.271
		S	01.09.07	o386	9	2.5	-7.75	0.10	0.12	-7.74	0.19	0.07	1 m.	7.83	3 m.	-12.31	1.0357	3.38	7.5	-	-	-	-	-	-	-
		U	02.15.07	o387	25	4.4	-7.94	0.10	0.08	-7.48	0.10	0.07	1 m.	6.31	3 m.	-12.38	1.0360	3.36	6.5	-	-	-	-	-	-	-
		W	03.12.07	o388	18	3.4	-7.80	0.12	0.12	-7.44	0.19	0.07	1 m.	6.23	3 m.	-12.31	1.0360	3.32	6.5	-	-	-	-	-	-	-
		Y	04.10.07	o389	19	3.4	-7.83	0.08	0.12	-7.49	0.14	0.07	1 m.	6.74	3 m.	-12.31	1.0360	3.39	6.7	1 m.	0.213	0.00288	0.0135	0.00486	0.001261	0.260
		aa	05.01.07	o390	13	2.5	-7.52	0.13	0.12	-7.40	0.15	0.07	1 m.	7.00	3 m.	-12.21	1.0359	3.43	6.7	-	-	-	-	-	-	-
Adult all values																									
13	Af	A	04.07.06	o294	2	2.9	-7.94	0.22	0.07	-7.25	0.15	0.07	3 m.	4.93	2 m.	-12.51	1.0364	3.41	5.2	1 m.	0.210	0.00328	0.0156	0.00451	0.00127	0.282
		B	04.19.06	o260	4	6.2	-6.96	0.06	0.06	-6.99	0.12	0.08	3 m.	5.16	2 m.	-12.51	1.0367	3.73	4.4	1 m.	0.210	0.00306	0.0146	0.00451	0.00132	0.292
				o261	4	6.4	-7.54	0.08	0.06	-6.95	0.07	0.08	3 m.	5.16	2 m.	-12.51	1.0367	3.77	4.3	-	-	-	-	-	-	-
				o262	6	8.6	-7.37	0.05	0.06	-7.04	0.08	0.08	3 m.	5.16	2 m.	-12.51	1.0366	3.67	4.6	-	-	-	-	-	-	-
		D	05.16.06	o295	2	3.0	-7.62	0.17	0.07	-7.30	0.14	0.07	3 m.	6.28	2 m.	-12.51	1.0364	3.67	5.4	-	-	-	-	-	-	-
		R	12.12.06	o296	4	3.0	-5.82	0.13	0.07	-8.28	0.20	0.07	1 w.	9.08	sampl.	-12.21	1.0350	3.00	9.7	sampl.	-	-	-	0.00496	0.00156	0.314
		T	01.16.07	o263	6	8.0	-6.25	0.08	0.06	-7.56	0.08	0.08	1 m.	7.83	1 m.	-12.21	1.0358	3.46	7.3	-	-	-	-	-	-	-
				o264	6	5.6	-6.46	0.07	0.06	-7.51	0.12	0.08	1 m.	7.83	1 m.	-12.21	1.0358	3.51	7.1	sampl.	-	-	-	0.00490	0.00147	0.299
				o265	6	6.3	-6.25	0.09	0.06	-7.63	0.11	0.08	1 m.	7.83	1 m.	-12.21	1.0357	3.39	7.5	sampl.	-	-	-	0.00490	0.00136	0.277
				o297	6	4.1	-6.01	0.15	0.07	-7.66	0.14	0.07	1 m.	7.83	1 m.	-12.21	1.0357	3.35	7.6	-	-	-	-	-	-	-
				o298	4	4.1	-7.31	0.10	0.07	-7.83	0.12	0.07	1 m.	7.83	1 m.	-12.21	1.0355	3.18	8.2	sampl.	0.204	0.00320	0.0157	0.00490	0.00136	0.278
		V	02.20.07	o266	6	7.1	-7.05	0.09	0.06	-7.76	0.09	0.08	3 m.	7.63	2 m.	-12.21	1.0356	3.20	8.0	-	-	-	-	-	-	-
				o267	5	6.9	-6.87	0.07	0.06	-7.52	0.13	0.08	3 m.	7.63	2 m.	-12.21	1.0358	3.46	7.1	-	-	-	-	-	-	-
				o268	5	6.4	-6.77	0.06	0.06	-7.39	0.09	0.08	3 m.	7.63	2 m.	-12.21	1.0359	3.58	6.7	-	-	-	-	-	-	-

Table AII.4. *Candona neglecta*

Adult all values																								
13	Af	X	03.27.07	o269	6	7.9	-7.25	0.09	0.06	-7.54	0.06	0.08	3 m.	6.65	2 m.	-12.23	1.0358	3.23	7.1	-	-	-	-	-	-	-
				o270	6	8.4	-7.51	0.11	0.06	-7.78	0.13	0.08	3 m.	6.65	2 m.	-12.23	1.0356	2.98	7.9	-	-	-	-	-	-	-
				o271	6	8.5	-7.03	0.04	0.06	-7.45	0.08	0.08	3 m.	6.65	2 m.	-12.23	1.0359	3.33	6.8	-	-	-	-	-	-	-
				o272	4	5.4	-7.95	0.14	0.06	-7.55	0.20	0.08	3 m.	6.65	2 m.	-12.23	1.0358	3.22	7.2	-	-	-	-	-	-	-
		Z	04.25.07	o273	4	5.3	-7.74	0.13	0.06	-7.49	0.13	0.08	3 m.	7.05	2 m.	-12.17	1.0358	3.31	7.2	1 m.	0.215	0.00380	0.0177	0.00484	0.00122	0.252
	Am	B	04.19.06	o136	2	3.5	-7.01	0.13	0.18	-7.43	0.12	0.14	3 m.	5.16	2 m.	-12.51	1.0362	3.27	5.9	1 m.	-	-	-	0.00451	0.00117	0.259
		R	12.12.06	o137	6	5.0	-5.01	0.11	0.16	-8.02	0.11	0.14	1 w.	9.08	sampl.	-12.21	1.0353	3.28	8.8	sampl.	-	-	-	0.00496	0.00156	0.315
				o138	4	6.4	-6.26	0.10	0.07	-8.53	0.10	0.10	1 w.	9.08	sampl.	-12.21	1.0347	2.74	10.6	sampl.	-	-	-	0.00496	0.00137	0.276
		T	01.16.07	o139	4	5.7	-7.39	0.08	0.07	-7.94	0.09	0.10	1 m.	7.83	1 m.	-12.21	1.0354	3.06	8.6	sampl.	-	-	-	0.00490	0.00130	0.265
				o140	4	5.8	-6.54	0.14	0.07	-7.65	0.07	0.10	1 m.	7.83	1 m.	-12.21	1.0357	3.36	7.6	sampl.	-	-	-	0.00490	0.00136	0.278
				o141	4	6.5	-6.86	0.14	0.07	-7.85	0.13	0.10	1 m.	7.83	1 m.	-12.21	1.0355	3.16	8.2	sampl.	-	-	-	0.00490	0.00134	0.274
				o142	2	3.4	-6.97	0.25	0.18	-8.04	0.18	0.14	1 m.	7.83	1 m.	-12.21	1.0353	2.96	8.9	sampl.	-	-	-	0.00490	0.00130	0.265
				o143	2	3.0	-6.97	0.12	0.13	-7.99	0.19	0.19	1 m.	7.83	1 m.	-12.21	1.0353	3.01	8.7	sampl.	-	-	-	0.00490	0.00131	0.266
		V	02.20.07	o144	4	7.0	-6.65	0.07	0.07	-7.56	0.12	0.10	3 m.	7.63	2 m.	-12.21	1.0358	3.41	7.3	1 m.	-	-	-	0.00490	0.00125	0.256
		X	03.27.07	o145	4	6.1	-7.53	0.12	0.07	-7.70	0.10	0.10	3 m.	6.65	2 m.	-12.23	1.0356	3.06	7.7	1 m.	-	-	-	0.00481	0.00134	0.278
				o146	4	4.8	-6.41	0.12	0.16	-7.32	0.15	0.14	3 m.	6.65	2 m.	-12.23	1.0360	3.45	6.4	1 m.	-	-	-	0.00481	0.00132	0.274
		Z	04.25.07	o147	2	2.7	-6.25	0.11	0.13	-7.50	0.17	0.19	3 m.	7.05	2 m.	-12.17	1.0358	3.31	7.2	1 m.	-	-	-	0.00484	0.00125	0.258
Adult monthly averages																								
	Af	A	04.07.06				-7.94			-7.25			3 m.	4.93	2 m.	-12.51	1.0364	3.45	5.2	1 m.	0.210	0.00328	0.0156	0.00451	0.001272	0.282
		B	04.19.06				-7.29			-6.99			3 m.	5.16	2 m.	-12.51	1.0367	3.87	4.4	1 m.	0.210	0.00306	0.0146	0.00451	0.00132	0.292
		D	05.16.06				-7.62			-7.30			3 m.	6.28	2 m.	-12.51	1.0364	4.10	5.4	-	-	-	-	-	-	-
		R	12.12.06				-5.82			-8.28			1 w.	9.08	sampl.	-12.21	1.0350	3.28	9.7	sampl.	-	-	-	0.00496	0.001556	0.314
		T	01.16.07				-6.46			-7.64			1 m.	7.83	1 m.	-12.21	1.0357	3.38	7.5	sampl.	0.204	0.00320	0.0157	0.00490	0.001396	0.285
		V	02.20.07				-6.90			-7.56			3 m.	7.63	2 m.	-12.21	1.0358	3.09	7.3	-	-	-	-	-	-	-
		X	03.27.07				-7.43			-7.58			3 m.	6.65	2 m.	-12.23	1.0358	3.20	7.3	-	-	-	-	-	-	-
		Z	04.25.07				-7.74			-7.49			3 m.	7.05	2 m.	-12.17	1.0358	3.55	7.2	1 m.	0.215	0.00380	0.0177	0.00484	0.001221	0.252
	Am	B	04.19.06				-7.01			-7.43			3 m.	5.16	2 m.	-12.51	1.0362	3.27	5.9	1 m.	-	-	-	0.00451	0.00117	0.259
		R	12.12.06				-5.64			-8.27			1 w.	9.08	sampl.	-12.21	1.0350	3.01	9.7	sampl.	-	-	-	0.00496	0.001465	0.295
		T	01.16.07				-6.95			-7.90			1 m.	7.83	1 m.	-12.21	1.0354	3.11	8.4	sampl.	-	-	-	0.00490	0.001321	0.270
		V	02.20.07				-6.65			-7.56			3 m.	7.63	2 m.	-12.21	1.0358	3.41	7.3	1 m.	-	-	-	0.00490	0.001254	0.256
		X	03.27.07				-6.97			-7.51			3 m.	6.65	2 m.	-12.23	1.0358	3.26	7.0	1 m.	-	-	-	0.00481	0.001328	0.276
		Z	04.25.07				-6.25			-7.50			3 m.	7.05	2 m.	-12.17	1.0358	3.31	7.2	1 m.	-	-	-	0.00484	0.001251	0.258
Juveniles all values																								
	A-1f	R	12.12.06	o286	14	6.9	-5.69	0.09	0.06	-8.16	0.10	0.08	2 w.	9.84	sampl.	-12.21	1.0351	3.30	9.3	sampl.	0.197	0.00278	0.0141	0.00496	0.00145	0.292
		T	01.16.07	o287	15	7.6	-6.27	0.09	0.06	-7.58	0.06	0.08	2 w.	7.31	sampl.	-12.23	1.0358	3.34	7.3	sampl.	0.204	0.00250	0.0123	0.00490	0.001366	0.279
		V	02.20.07	o311	6	2.5	-6.77	0.14	0.13	-7.28	0.22	0.09	2 w.	6.24	sampl.	-12.17	1.0360	3.34	6.5	sampl.	-	-	-	0.00481	0.001232	0.256
	A-1m	R	12.12.06	o325	6	2.8	-6.32	0.16	0.04	-8.72	0.21	0.08	2 w.	9.84	sampl.	-12.21	1.0346	2.73	11.2	sampl.	-	-	-	0.00496	0.001483	0.299
		T	01.16.07	o326	7	4.0	-6.29	0.14	0.04	-7.70	0.15	0.08	2 w.	7.31	sampl.	-12.23	1.0357	3.22	7.6	sampl.	-	-	-	0.00490	0.001521	0.310
		V	02.20.07	o327	4	2.2	-6.91	0.15	0.04	-7.44	0.25	0.08	2 w.	6.24	sampl.	-12.17	1.0359	3.18	7.0	sampl.	-	-	-	0.00481	0.001394	0.290
	A-2	H	07.11.06	o372	10	2.9	-5.83	0.11	0.11	-9.11	0.16	0.07	1 m.	12.74	sampl.	-12.39	1.0343	3.18	11.9	sampl.	-	-	-	0.00419	0.001519	0.363
		J	08.10.06	o373	16	4.5	-5.61	0.11	0.08	-9.43	0.10	0.07	2 m.	13.45	1 m.	-12.39	1.0340	3.00	13.0	1 m.	-	-	-	0.00419	0.001373	0.328
		L	09.12.06	o374	26	7.8	-5.95	0.08	0.08	-9.67	0.07	0.07	3 m.	13.85	2 m.	-12.39	1.0338	2.85	13.8	1 m.	0.243	0.00382	0.0157	0.00486	0.001313	0.270
		N	10.10.06	o375	24	8.1	-6.20	0.11	0.08	-9.77	0.08	0.07	4 m.	13.93	3 m.	-12.39	1.0337	2.76	14.2	-	-	-	-	-	-	-
Adult all values																								
6	Am	A	04.07.06	o135	2	4.5	-7.43	0.09	0.16	-7.00	0.08	0.14	3 m.	5.03	2 m.	-12.13	1.0363	3.29	5.7	-	-	0.00380	-	-	0.00133	-

TABLE AII.5
Geochemical composition of *Fabaeformiscandona caudata*.

depth	age & sex	sampling	ananlyse identifier	nbr. of vavles	area 44/45/ 46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)					(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
13	Ad	B 04.19.06	o277	4	4.5	-7.24	0.10	0.06	-7.45	0.15	0.08	1 m.	5.8	1 m.	-12.51	1.0362	3.40	5.4	1 m.	0.210	0.00399	0.0190	0.00451	0.00125	0.277
		D 05.16.06	o278	7	7.7	-5.12	0.18	0.06	-8.11	0.08	0.08	1 m.	8.1	1 m.	-12.54	1.0355	3.30	7.7	-	-	-	-	-	-	-
			o340	4	3.9	-6.94	0.10	0.18	-7.98	0.11	0.15	1 m.	8.1	1 m.	-12.54	1.0357	3.43	7.2	-	-	-	-	-	-	-
		F 06.12.06	o279	5	6.2	-5.96	0.12	0.06	-8.56	0.05	0.08	1 m.	9.5	1 m.	-12.45	1.0350	3.07	9.6	1 m.	0.210	0.00398	0.0189	0.00398	0.00125	0.314
		J 08.10.06	o341	2	2.3	-5.44	0.13	0.18	-10.27	0.12	0.15	1 m.	14.2	1 m.	-12.39	1.0331	2.30	16.2	-	-	-	-	-	0.00147	-
		R 12.12.06	o342	4	3.6	-6.98	0.13	0.18	-8.72	0.13	0.15	1 m.	10.3	1 m.	-12.26	1.0346	2.88	10.9	-	-	-	-	-	0.00130	-
		T 01.16.07	o280	6	6.3	-6.19	0.08	0.06	-8.30	0.13	0.08	1 m.	7.8	1 m.	-12.21	1.0350	2.70	9.6	-	-	-	-	-	-	-
		X 03.27.07	o343	2	2.3	-5.52	0.15	0.18	-8.99	0.21	0.15	?	?	1 m.	-12.17	1.0342	-	12.2	-	-	-	-	-	-	-
		Z 04.25.07	o281	6	6.6	-5.95	0.12	0.06	-8.03	0.12	0.08	1 m.	8.1	1 m.	-12.23	1.0353	3.05	8.5	1 m.	0.215	0.00324	0.0151	0.00484	0.00137	0.283
	A-1	N 10.10.06	o349	4	1.5	-4.93	0.22	0.21	-9.31	0.25	0.14	2 w.	13.8	sampl.	-12.38	1.0341	3.46	12.6	sampl.	-	-	-	0.00425	0.00131	0.310
		R 12.12.06	o350	4	1.7	-6.31	0.27	0.21	-8.50	0.28	0.14	2 w.	9.8	sampl.	-12.21	1.0348	3.05	10.3	sampl.	-	-	-	0.00496	0.00127	0.256
		X 03.27.07	o351	5	1.8	-4.02	0.26	0.21	-7.52	0.22	0.14	2 w.	6.9	sampl.	-12.23	1.0358	3.26	6.7	sampl.	-	-	-	0.00484	0.00136	0.281
		A+B	o347	6	2.0	-6.26	0.16	0.21	-7.57	0.22	0.14	2 w.	5.8	sampl.	-12.52	1.0361	3.21	5.8	sampl.	-	-	-	0.00456	0.00139	0.305
		H+J	o348	4	2.0	-6.46	0.17	0.21	-9.22	0.22	0.14	2 w.	13.8	sampl.	-12.35	1.0342	3.18	12.4	sampl.	-	-	-	0.00453	0.00136	0.299
	A-2	B 04.19.06	o409	2	0.5	-7.01	0.65	0.16	-6.62	1.72	0.14	O.T.	-	1 m.	-12.51	1.0371	-	2.5	-	-	-	-	-	-	-
		F 06.12.06	o410	2	0.5	-5.28	0.55	0.16	-7.86	0.58	0.14	2 m.	8.8	1 m.	-12.45	1.0357	3.79	7.1	-	-	-	-	-	-	-
		H 07.11.06	o411	8	2.0	-6.20	0.20	0.16	-9.18	0.20	0.14	2 m.	11.0	1 m.	-12.40	1.0343	3.10	12.1	1 m.	-	-	-	0.00430	0.00123	0.287
		J 08.10.06	o412	24	5.5	-5.56	0.04	0.08	-9.63	0.06	0.06	2 m.	13.5	1 m.	-12.39	1.0338	2.96	13.8	1 m.	0.208	0.00319	0.0153	0.00419	0.00116	0.277
		L 09.12.06	o413	19	5.1	-5.87	0.07	0.08	-9.41	0.14	0.06	2 m.	14.1	1 m.	-12.30	1.0339	3.08	13.3	1 m.	0.243	0.00348	0.0144	0.00486	0.00134	0.276
		N 10.10.06	o414	20	4.4	-5.78	0.12	0.08	-9.27	0.15	0.06	O.T.	-	08/06	-12.30	1.0341	-	12.8	-	-	-	-	-	-	-
		P 11.15.06	o415	13	3.2	-5.93	0.13	0.08	-9.42	0.09	0.06	O.T.	-	08/06	-12.30	1.0339	-	13.4	-	-	-	-	-	-	-
		R 12.12.06	o416	21	5.9	-6.60	0.12	0.08	-9.63	0.13	0.06	O.T.	-	08/06	-12.30	1.0337	-	14.2	-	-	-	-	-	-	-
		T 01.16.07	o417	22	4.8	-5.73	0.14	0.08	-9.36	0.10	0.06	O.T.	-	08/06	-12.30	1.0340	-	13.2	-	-	-	-	-	-	-
		V 02.20.07	o418	22	5.9	-6.01	0.07	0.08	-9.63	0.20	0.06	O.T.	-	08/06	-12.30	1.0337	-	14.1	-	-	-	-	-	-	-
		X 03.27.07	o419	10	2.4	-5.78	0.12	0.05	-9.62	0.25	0.03	O.T.	-	08/06	-12.30	1.0337	-	14.1	-	-	-	-	-	-	-
		Z 04.25.07	o420	4	1.1	-5.68	0.25	0.16	-9.39	0.33	0.14	O.T.	-	08/06	-12.30	1.0340	-	13.2	-	-	-	-	-	-	-

TABLE AII.6
Geochemical composition of *Pseudocandona compressa.*

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
6	Adm	C	04.25.06	o01	5	3.3	-4.19	0.15	0.08	-8.68	0.13	0.11	4 d.	10.8	sampl.	-12.41	1.0348	3.19	11.0	-	-	-	-	-	-	-
		E	05.24.06	o02	5	5.1	-4.97	0.09	0.07	-8.86	0.12	0.09	O.T.	-	04/06	-12.41	1.0346	-	11.7	-	-	-	-	-	-	-
		G	06.19.06	o03	5	4.6	-4.82	0.13	0.07	-9.35	0.15	0.15	4 d.	15.2	sampl.	-12.36	1.0341	3.44	13.9	-	-	-	-	-	-	-
		I	07.24.06	o04	5	4.0	-4.98	0.10	0.08	-11.46	0.13	0.10	4 d.	24.0	sampl.	-11.94	1.0314	2.73	24.3	-	-	-	-	-	-	-
		Y	04.10.07	o05	4	2.7	-3.89	0.20	0.15	-7.91	0.12	0.16	4 d.	9.1	sampl.	-12.15	1.0353	3.35	9.0	-	-	-	-	-	-	-
		aa	05.01.07	o06	5	3.9	-4.79	0.07	0.08	-8.48	0.13	0.12	4 d.	13.6	sampl.	-12.08	1.0347	3.71	11.5	-	-	-	-	-	-	-
	Ad	A	04.07.06	o659	8	3.0	-5.14	0.16	0.06	-7.85	0.20	0.07	O.T.	-	year	-12.30	1.0356	-	8.2	-	-	-	-	-	-	-
		C	04.25.06	o660	20	7.9	-4.60	0.10	0.12	-8.73	0.12	0.06	4 d.	10.8	sampl.	-12.41	1.0348	3.15	11.2	sampl.	0.2409	0.00307	0.013	0.00508	0.00150	0.296
		E	05.24.06	o661	20	13.9	-5.06	0.06	0.12	-9.18	0.08	0.06	O.T.	-	04/06	-12.41	1.0343	-	13.0	-	-	-	-	-	-	-
		I	07.24.06	o662	20	12.8	-5.15	0.06	0.12	-11.51	0.09	0.06	4 d.	24.0	sampl.	-11.94	1.0314	2.68	24.5	sampl.	0.2652	0.00493	0.019	0.00561	0.00138	0.246
		K	08.31.06	o663	24	16.7	-4.98	0.04	0.12	-10.73	0.05	0.06	O.T.	-	04/06	-12.41	1.0327	-	19.3	-	-	-	-	-	-	-
		M	10.04.06	o664	8	3.9	-5.44	0.17	0.08	-10.31	0.18	0.05	O.T.	-	04/06	-12.41	1.0331	-	17.5	-	-	-	-	-	-	-
		Q	11.28.06	o665	8	3.8	-5.55	0.09	0.08	-8.65	0.17	0.05	O.T.	-	04/06	-12.41	1.0348	-	10.9	-	-	-	-	-	-	-
		U+W		o658	4	1.9	-6.73	0.22	0.22	-7.51	0.15	0.07	O.T.	-	04/06	-12.41	1.0360	-	6.5	-	-	-	-	-	-	-
		Y	04.10.07	o666	20	8.1	-5.02	0.09	0.12	-8.01	0.09	0.06	4 d.	9.1	sampl.	-12.15	1.0352	3.24	9.4	sampl.	0.220	0.00286	0.0130	0.00416	0.00164	0.394
		aa	05.01.07	o667	20	11.3	-5.89	0.06	0.12	-8.94	0.08	0.06	4 d.	13.6	sampl.	-12.08	1.0342	3.23	13.4	sampl.	0.223	0.00407	0.018	0.00432	0.00141	0.327
	A-1m	A	04.07.06	o07	20	6.6	-5.39	0.10	0.07	-7.18	0.11	0.12	2 d.	6.6	sampl.	-12.13	1.0361	3.49	6.3	-	-	-	-	-	-	-
	A-1f	A	04.07.06	o08	15	5.6	-5.84	0.07	0.06	-7.25	0.12	0.10	2 d.	6.6	sampl.	-12.13	1.0360	3.42	6.6	-	-	-	-	-	-	-
	A-1	C	04.25.06	o09	20	8.1	-5.69	0.07	0.07	-8.20	0.08	0.08	2 d.	10.5	sampl.	-12.41	1.0353	3.63	9.1	-	-	-	-	-	-	-
		I	07.24.06	o10	20	5.7	-4.07	0.11	0.06	-11.51	0.12	0.11	2 d.	24.2	sampl.	-11.94	1.0314	2.71	24.5	-	-	-	-	-	-	-
		Y	04.10.07	o11	20	7.0	-5.41	0.11	0.07	-8.05	0.08	0.09	2 d.	9.7	sampl.	-12.15	1.0352	3.33	9.6	-	-	-	-	-	-	-
		aa	05.01.07	o12	20	7.7	-5.20	0.06	0.07	-9.71	0.08	0.07	2 d.	16.5	sampl.	-12.08	1.0334	3.07	16.4	-	-	-	-	-	-	-
	A-2	A	04.07.06	o13	20	7.8	-3.02	0.08	0.07	-10.77	0.08	0.08	O.T.	-	year	-12.30	1.0325	-	19.9	-	-	-	-	-	-	-
		C	04.25.06	o14	20	7.7	-3.46	0.09	0.07	-10.59	0.08	0.09	O.T.	-	year	-12.30	1.0327	-	19.2	-	-	-	-	-	-	-
		I	07.24.06	o15	20	6.8	-4.07	0.10	0.07	-11.29	0.11	0.10	2 w.	23.5	sampl.	-11.94	1.0316	2.79	23.6	-	-	-	-	-	-	-
		K	08.31.06	o16	20	7.2	-4.41	0.13	0.07	-9.95	0.08	0.06	1 m.	16.3	sampl.	-12.37	1.0334	3.06	16.2	-	-	-	-	-	-	-
		M	10.04.06	o17	20	7.7	-4.14	0.11	0.07	-10.56	0.08	0.10	3 m.	19.5	1 m.	-12.37	1.0328	3.14	18.7	-	-	-	-	-	-	-
		O	10.25.06	o18	20	7.6	-4.64	0.07	0.07	-10.84	0.08	0.07	O.T.	-	09/06	-12.42	1.0326	-	19.7	-	-	-	-	-	-	-
		O'	10.25.06	o19	20	7.6	-4.07	0.10	0.07	-11.20	0.08	0.11	O.T.	-	09/06	-12.42	1.0322	-	21.2	-	-	-	-	-	-	-
		Qs	11.28.06	o20	20	7.7	-4.24	0.09	0.07	-10.71	0.08	0.05	O.T.	-	09/06	-12.42	1.0327	-	19.1	-	-	-	-	-	-	-
		Qa	11.28.06	o21	20	7.4	-4.28	0.11	0.07	-11.16	0.08	0.08	O.T.	-	09/06	-12.42	1.0322	-	21.0	-	-	-	-	-	-	-
		Ss	01.09.07	o22	20	7.5	-4.24	0.08	0.07	-10.96	0.08	0.11	O.T.	-	09/06	-12.42	1.0324	-	20.2	-	-	-	-	-	-	-
		Sa	01.09.07	o23	20	7.2	-4.46	0.05	0.07	-10.81	0.08	0.11	O.T.	-	09/06	-12.42	1.0326	-	19.6	-	-	-	-	-	-	-
		Sa	01.09.07	o28	20	7.2	-4.32	0.08	0.07	-11.01	0.08	0.06	O.T.	-	09/06	-12.42	1.0324	-	20.4	-	-	-	-	-	-	-
		U	02.15.07	o24	20	7.0	-4.13	0.11	0.07	-10.58	0.08	0.06	O.T.	-	09/06	-12.42	1.0328	-	18.6	-	-	-	-	-	-	-
		W	03.12.07	o25	20	7.2	-4.39	0.08	0.07	-10.58	0.08	0.07	O.T.	-	09/06	-12.42	1.0328	-	18.6	-	-	-	-	-	-	-
		Y	04.10.07	o26	20	7.8	-4.25	0.05	0.07	-10.68	0.08	0.16	O.T.	-	09/06	-12.42	1.0327	-	19.0	-	-	-	-	-	-	-
		aa	05.01.07	o27	20	7.6	-4.15	0.08	0.07	-10.78	0.08	0.09	O.T.	-	09/06	-12.42	1.0326	-	19.4	-	-	-	-	-	-	-

3	Ad	C	04.25.06	o565	20	11.5	-5.11	0.05	0.07	-8.89	0.06	0.07	2 w.	9.7	sampl.	-12.52	1.0347	2.84	11.4	sampl.	0.251	0.00350	0.014	0.00515	0.00191	0.371
		C	04.25.06	o566	16	9.4	-4.92	0.08	0.07	-8.32	0.10	0.07	2 w.	9.7	sampl.	-12.52	1.0353	3.43	9.2	sampl.	0.251	0.00334	0.013	0.00515	0.00244	0.474
		E	05.24.06	o567	12	8.2	-4.47	0.06	0.07	-9.59	0.12	0.07	O.T.	-	04/06	-12.52	1.0340	-	14.2	-	-	-	-	-	-	-
		I	07.24.06	o568	13	8.0	-4.45	0.06	0.07	-11.76	0.10	0.07	2 w.	25.5	sampl.	-11.91	1.0311	2.68	25.8	sampl.	0.279	0.00618	0.022	0.00575	0.00174	0.303
		K	08.31.06	o569	10	6.4	-3.87	0.12	0.07	-11.09	0.12	0.07	O.T.	-	04/06	-12.52	1.0324	-	20.3	-	-	-	-	-	-	-
		Y	04.10.07	o570	21	9.0	-4.42	0.07	0.07	-8.38	0.10	0.07	2 w.	9.4	sampl.	-12.09	1.0348	2.87	11.1	sampl.	0.216	0.00301	0.014	0.00493	0.00174	0.354
		aa	05.01.07	o668	20	13.5	-5.93	0.03	0.12	-9.67	0.07	0.06	2 w.	16.8	sampl.	-12.07	1.0334	3.17	16.3	sampl.	0.231	0.00397	0.017	0.00482	0.00154	0.320
	A-1	C	04.25.06	o682	25	5.47	-2.47	0.09	0.06	-9.47	0.16	0.07	4 d.	13.4	sampl.	-12.52	1.0341	3.09	13.7	sampl.	0.251	0.00359	0.014	0.00515	0.001787	0.347
		W	03.12.07	o683	23	4.93	-6.23	0.09	0.06	-7.46	0.12	0.07	4 d.	6.9	sampl.	-12.07	1.0357	3.20	7.6	sampl.	0.216	0.00233	0.011	0.00446	0.001425	0.320
		Y	04.10.07	o684	21	4.67	-5.48	0.11	0.06	-8.26	0.16	0.07	4 d.	10.6	sampl.	-12.09	1.0349	3.26	10.6	sampl.	0.216	0.002901	0.013	0.00493	0.001532	0.311
	A-2	C	04.25.06	o685	32	6.96	-2.71	0.11	0.06	-10.86	0.30	0.07	O.T.	-	year	-12.40	1.0325	-	19.9	-	-	-	-	-	-	-
		I	07.24.06	o634	9	1.97	-3.39	0.22	0.23	-11.72	0.24	0.16	2 w.	25.5	sampl.	-11.91	1.0311	2.73	25.6	sampl.	-	-	-	0.00575	0.001767	0.307
		K	08.31.06	o635	12	2.27	-3.39	0.19	0.31	-11.33	0.27	0.14	2 m.	21.5	sampl.	-12.38	1.0320	2.77	21.9	sampl.	0.232	0.004327	0.019	0.00486	0.001399	0.288
		O	10.25.06	o686	40	8.95	-3.38	0.04	0.06	-10.66	0.07	0.07	3 m.	18.5	1 m.	-12.44	1.0328	2.89	18.8	1 m.	0.225	0.003999	0.018	0.00511	0.001559	0.305
		Q	11.28.06	o687	30	7.14	-4.11	0.08	0.06	-10.65	0.11	0.07	O.T	-	09/06	-12.38	1.0327	-	19.1	-	-	-	-	-	-	-
		U	02.15.07	o688	36	7.45	-3.90	0.08	0.06	-10.05	0.12	0.07	O.T	-	09/06	-12.38	1.0333	-	16.6	-	-	-	-	-	-	-
		W	03.12.07	o689	40	7.78	-4.03	0.07	0.06	-10.88	0.11	0.07	O.T	-	09/06	-12.38	1.0325	-	20.0	-	-	-	-	-	-	-

TABLE AII.7
Geochemical composition of *Cypria ophtalmica*.

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
70	Ad	D	04.19.06	o205	25	5.5	-8.10	0.09	0.04	-8.68	0.09	0.14	6 m.	5.0	2 m.	-12.64	1.0350	2.07	5.1	1 m.	0.211	0.00739	0.0074	0.00371	0.00197	0.530
				o678	36	5.7	-8.28	0.11	0.06	-8.72	0.09	0.07	6 m.	5.0	2 m.	-12.64	1.0350	2.03	5.2	-	-	-	-	-	-	-
		F	06.12.06	o206	26	5.7	-8.26	0.11	0.04	-8.63	0.14	0.08	6 m.	4.9	2 m.	-12.64	1.0351	2.11	4.9	2 m.	0.213	0.00746	0.0075	0.00381	0.00191	0.514
				o631	16	2.2	-7.73	0.29	0.31	-8.54	0.45	0.14	6 m.	4.9	2 m.	-12.64	1.0352	2.20	4.5	2 m.	0.213	0.00546	0.0055	0.00381	0.00188	0.506
		J	08.16.06	o207	11	2.4	-7.50	0.22	0.10	-8.42	0.28	0.15	6 m.	5.1	2 m.	-12.58	1.0353	2.31	4.3	2 m.	0.217	0.00820	0.0082	0.00463	0.00179	0.478
		L	09.12.06	o632	6	1.0	-7.13	0.51	0.23	-8.51	0.64	0.16	6 m.	5.2	2 m.	-12.33	1.0349	1.99	5.6	2 m.	-	-	-	0.00374	0.00188	0.443
		N	10.10.06	o208	23	4.8	-8.18	0.09	0.04	-8.75	0.15	0.14	6 m.	5.4	2 m.	-12.39	1.0347	1.86	6.2	2 m.	0.215	0.00716	0.0072	0.00365	0.00197	0.420
		P	11.15.06	o209	12	2.6	-8.15	0.20	0.10	-8.73	0.25	0.15	6 m.	5.6	2 m.	-12.45	1.0348	1.97	5.9	2 m.	0.213	0.00889	0.0089	0.00376	0.00171	0.470
		R	12.12.06	o210	23	4.4	-8.40	0.10	0.04	-8.44	0.22	0.14	6 m.	5.7	2 m.	-12.34	1.0350	2.18	5.3	2 m.	0.212	0.00745	0.0075	0.00375	0.00187	0.499
				o679	41	5.4	-8.32	0.12	0.06	-8.59	0.12	0.07	6 m.	5.7	2 m.	-12.34	1.0348	2.03	5.8	-	-	-	-	-	-	-
		T	01.16.07	o211	36	7.5	-8.32	0.09	0.04	-8.54	0.18	0.08	6 m.	5.7	2 m.	-12.29	1.0348	2.03	5.8	2 m.	0.214	0.00685	0.0069	0.00454	0.00184	0.490
				o680	20	2.9	-8.19	0.12	ND	-8.41	0.21	ND	6 m.	5.7	2 m.	-12.29	1.0350	2.16	5.3	2 m.	0.214	0.00497	0.0050	0.00454	0.00194	0.516
		V	02.20.07	o212	24	4.7	-8.32	0.11	0.04	-8.52	0.19	0.14	6 m.	5.7	2 m.	-12.28	1.0348	2.04	5.8	2 m.	0.213	0.00612	0.0061	0.00355	0.00191	0.420
		X	03.27.07	o213	31	6.8	-8.09	0.06	0.04	-8.55	0.12	0.08	6 m.	5.8	2 m.	-12.21	1.0347	1.97	6.2	2 m.	0.213	0.00588	0.0059	0.00361	0.00208	0.586
				o681	37	5.2	-8.25	0.08	0.06	-8.35	0.30	0.07	6 m.	5.8	2 m.	-12.21	1.0349	2.18	5.4	-	-	-	-	-	-	-
		Z	04.25.07	o214	24	5.0	-8.42	0.13	0.04	-8.59	0.22	0.14	6 m.	6.0	2 m.	-12.33	1.0348	2.09	5.9	2 m.	0.212	0.00597	0.0060	0.00373	0.00194	0.537
				o633	12	1.9	-7.98	0.22	0.23	-8.41	0.17	0.16	6 m.	6.0	2 m.	-12.33	1.0350	2.28	5.2	2 m.	0.212	0.00621	0.0062	0.00373	0.00188	0.522
13	Ad	D	05.10.06	o624	12	2.4	-6.46	0.24	0.31	-10.35	0.18	0.14	O.T.	-	year	-12.40	1.0331	-	12.3	O.T.	-	0.00446	0.0045	-	0.00182	-
		F	06.12.06	o674	26	4.7	-7.49	0.12	0.06	-10.83	0.13	0.07	O.T.	-	year	-12.40	1.0326	-	14.2	O.T.	-	0.00531	0.0053	-	0.00183	-
		J	08.16.06	o625	4	0.8	-6.96	0.33	0.23	-10.48	0.90	0.16	3 m.	12.4	2 m.	-12.40	1.0329	1.70	12.8	2 m.	-	-	-	0.00430	0.00182	0.435
		L	09.12.06	o626	12	2.1	-6.91	0.15	0.31	-10.64	0.26	0.14	4m.	12.6	2 m.	-12.39	1.0327	1.58	13.5	2 m.	-	-	-	0.00419	0.00179	0.369
		N	10.10.06	o627	13	3.0	-7.36	0.14	0.18	-10.68	0.22	0.05	4m.	13.9	2 m.	-12.30	1.0326	1.73	14.0	2 m.	0.243	0.00424	0.0042	0.00486	0.00168	0.427
		P	11.15.06	o628	10	2.1	-7.31	0.13	0.31	-10.26	0.75	0.14	4m.	14.4	2 m.	-12.28	1.0330	2.23	12.4	2 m.	-	-	-	0.00392	0.00183	0.432
		R	12.12.06	o629	15	3.3	-7.43	0.14	0.18	-10.73	0.25	0.05	4m.	13.4	2 m.	-12.38	1.0326	1.65	13.8	2 m.	0.227	0.00513	0.0051	0.00425	0.00164	0.330
		T	01.16.07	o630	4	0.9	-7.51	0.59	0.23	-10.24	0.74	0.16	4m.	11.6	2 m.	-12.26	1.0330	1.63	12.4	2 m.	-	-	-	0.00495	0.00181	0.364
		V	02.20.07	o675	34	6.9	-7.38	0.06	0.06	-10.62	0.17	0.07	O.T.	-	year	-12.40	1.0328	-	13.4	O.T.	-	0.00436	0.0044	-	0.00173	-
		X	03.27.07	o676	31	6.2	-7.35	0.06	0.06	-10.38	0.11	0.07	O.T.	-	year	-12.40	1.0330	-	12.4	O.T.	-	0.00453	0.0045	-	0.00172	-
		Z	04.25.07	o677	26	4.7	-7.52	0.09	0.06	-10.20	0.14	0.07	O.T.	-	year	-12.40	1.0332	-	11.7	O.T.	-	0.00458	0.0046	-	0.00178	-

TABLE AII.8
Geochemical composition of *Prionocypris zenkeri.*

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
6	Ad	A	04.07.06	o655	1	3.2	-5.94	0.12	0.08	-7.31	0.19	0.05	3 w.	5.6	sampl.	-12.13	1.0359	3.12	4.4	sampl.	-	-	-	0.00454	0.00118	0.256
				o671	1	4.7	-4.37	0.08	0.12	-8.53	0.14	0.06	3 w.	5.6	sampl.	-12.13	1.0347	1.85	9.8	sampl.	-	-	-	0.00454	0.00118	0.261
		G	06.19.06	o647	1	5.7	-4.21	0.12	0.12	-9.43	0.16	0.06	3 w.	14.1	sampl.	-12.36	1.0340	3.12	12.7	sampl.	0.234	0.00317	0.014	0.00466	0.00134	0.286
				o672	1	5.0	-4.30	0.13	0.06	-9.42	0.17	0.07	3 w.	14.1	sampl.	-12.36	1.0340	3.14	12.7	sampl.	0.234	0.00375	0.016	0.00466	0.00120	0.258
		I	07.24.06	o656	1	2.3	-3.48	0.09	0.06	-11.17	0.17	0.07	3 w.	23.4	sampl.	-11.94	1.0317	2.89	22.9	sampl.	-	-	-	0.00561	0.00140	0.249
				o657	1	2.2	-3.90	0.20	0.06	-11.76	0.16	0.07	3 w.	23.4	sampl.	-11.94	1.0311	2.28	25.8	sampl.	-	-	-	0.00561	0.00138	0.245
3	Ad	E	05.24.06	o653	1	3.5	-4.31	0.18	0.08	-8.92	0.16	0.05	3 w.	12.4	sampl.	-12.42	1.0346	3.32	10.2	sampl.	0.221	0.00323	0.015	0.00473	0.00140	0.295
				o654	1	3.2	-4.01	0.08	0.08	-8.93	0.14	0.05	3 w.	12.4	sampl.	-12.42	1.0346	3.31	10.2	sampl.	-	-	-	0.00473	0.00133	0.281
		G	06.19.06	o669	1	5.0	-3.91	0.08	0.12	-10.07	0.10	0.06	3 w.	15.4	sampl.	-12.35	1.0333	2.74	15.7	sampl.	0.232	0.00266	0.011	0.00489	0.00136	0.277
				o670	1	5.4	-3.77	0.11	0.12	-10.04	0.12	0.06	3 w.	15.4	sampl.	-12.35	1.0333	2.76	15.6	sampl.	0.232	0.00266	0.011	0.00489	0.00138	0.282
	A-1	aa	05.01.07	o673	1	5.9	-4.89	0.11	0.06	-10.22	0.11	0.07	3 w.	15.8	sampl.	-12.07	1.0328	2.38	17.8	sampl.	0.231	0.00327	0.014	0.00482	0.00152	0.314

TABLE AII.9
Geochemical composition of *Herpetocypris reptans.*

depth	age & sex	sampling	ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	gene-ration	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)					(mV)	(‰VPDB)			(‰VPDB)					°C		(‰VSMOW)		(‰)	(°C)		molar ratio			molar ratio		
All values																										
13	Ad	A 04.07.06	o56	1	8.5	-7.74	0.05	0.05	-8.22	0.06	0.08	w	3 w.	5.2	sampl.	-12.51	1.0354	2.47	5.7	sampl.	0.210	0.00451	0.0215	0.00451	0.00093	0.205
			o57	1	9.2	-6.73	0.06	0.05	-10.32	0.08	0.08	ts	O.T.	-	year	-12.40	1.0331	-	14.9	-	-	-	-	-	-	-
			o112	1	10.1	-7.42	0.05	0.05	-10.20	0.10	0.08	ts	O.T.	-	year	-12.40	1.0332	-	14.3	-	-	-	-	-	-	-
		B 04.19.06	o58	1	7.6	-7.65	0.09	0.05	-8.09	0.08	0.08	w	3 w.	6.0	sampl.	-12.54	1.0356	2.82	5.1	sampl.	0.212	0.00445	0.0210	0.00461	0.00097	0.209
			o59	1	11.1	-7.05	0.06	0.05	-10.24	0.16	0.08	s	O.T.	-	year	-12.40	1.0332	-	14.5	-	-	-	-	-	-	-
			o113	1	11.8	-7.19	0.06	0.05	-9.55	0.06	0.08	s	O.T.	-	year	-12.40	1.0339	-	11.6	-	-	-	-	-	-	-
			o60	1	8.4	-7.33	0.08	0.05	-9.71	0.08	0.08	s	O.T.	-	year	-12.40	1.0337	-	12.3	-	-	-	-	-	-	-
			o61	1	7.7	-7.45	0.08	0.05	-10.23	0.11	0.08	ts	O.T.	-	year	-12.40	1.0332	-	14.5	-	-	-	-	-	-	-
			o114	1	8.9	-8.01	0.05	0.05	-8.38	0.12	0.08	w	3 w.	6.0	sampl.	-12.54	1.0353	2.52	6.2	sampl.	0.212	0.00596	0.0281	0.00461	0.00096	0.207
			o115	1	11.5	-7.54	0.07	0.05	-8.58	0.08	0.08	w	3 W.	6.0	sampl.	-12.54	1.0351	2.32	7.0	sampl.	0.212	0.00549	0.0259	0.00461	0.00104	0.225
			o116	1	11.2	-8.10	0.06	0.05	-7.98	0.06	0.08	w	3 w.	6.0	sampl.	-12.54	1.0357	2.94	4.6	sampl.	0.212	0.00514	0.0242	0.00461	0.00096	0.209
			o117	1	11.1	-7.49	0.06	0.05	-8.58	0.12	0.08	w	3 w.	6.0	sampl.	-12.54	1.0350	2.31	7.0	sampl.	0.212	0.00543	0.0256	0.00461	0.00103	0.222
		F 06.12.06	o62	1	7.7	-6.29	0.08	0.05	-8.67	0.07	0.08	w	O.T.	-	year	-12.40	1.0348	-	8.0	-	-	-	-	-	-	-
			o63	1	7.2	-7.14	0.06	0.05	-9.60	0.10	0.08	ts	O.T.	-	sampl.	-12.40	1.0338	-	11.8	-	-	-	-	-	-	-
			o64	1	7.9	-5.00	0.05	0.05	-9.35	0.10	0.08	w	O.T.	-	year	-12.40	1.0341	-	10.8	-	-	-	-	-	-	-
		H 07.11.06	o65	1	9.3	-8.32	0.06	0.05	-8.05	0.09	0.08	w	O.T.	-	year	-12.40	1.0355	-	5.5	-	-	-	-	-	-	-
		L 09.12.06	o66	1	8.3	-6.96	0.08	0.05	-10.04	0.15	0.08	s	3 w.	14.9	sampl.	-12.28	1.0333	2.59	14.2	sampl.	0.242	0.00470	0.0194	0.00392	0.00105	0.268
			o67	1	10.7	-7.38	0.05	0.05	-10.69	0.08	0.08	s	3 w.	14.9	sampl.	-12.28	1.0326	1.92	17.0	sampl.	0.242	0.00619	0.0256	0.00392	0.00105	0.269
			o118	1	12.4	-6.91	0.06	0.05	-10.00	0.09	0.08	s	3 w.	14.9	sampl.	-12.28	1.0333	2.64	14.0	sampl.	0.242	0.00487	0.0201	0.00392	0.00105	0.267
		N 10.10.06	o68	1	10.3	-7.42	0.06	0.05	-10.34	0.11	0.08	s	3 w.	14.6	sampl.	-12.38	1.0330	2.31	15.0	sampl.	0.227	0.00589	0.0260	0.00425	0.00109	0.257
			o69	1	10.7	-7.46	0.04	0.05	-10.53	0.12	0.08	s	3 w.	14.6	sampl.	-12.38	1.0329	2.11	15.8	sampl.	0.227	0.00603	0.0266	0.00425	0.00109	0.257
			o70	1	11.4	-7.38	0.07	0.05	-10.40	0.07	0.08	s	3 w.	14.6	sampl.	-12.38	1.0330	2.24	15.3	sampl.	0.227	0.00586	0.0259	0.00425	0.00104	0.246
			o119	1	10.3	-6.59	0.06	0.05	-10.50	0.09	0.08	ts	N.C.	-	sampl.	-12.38	1.0329	-	15.7	sampl.	0.227	0.00586	0.0259	0.00425	0.00103	0.243
		P 11.15.06	o71	1	8.9	-7.27	0.08	0.05	-10.19	0.11	0.08	s	O.T.	-	year	-12.40	1.0332	-	14.3	-	-	-	-	-	-	-
			o120	1	15.2	-7.39	0.06	0.05	-10.19	0.08	0.08	s	O.T.	-	year	-12.40	1.0332	-	14.3	-	-	-	-	-	-	-
			o121	1	8.8	-5.91	0.08	0.05	-10.24	0.06	0.08	ts	O.T.	-	year	-12.40	1.0332	-	14.5	-	-	-	-	-	-	-
			o72	1	8.8	-6.57	0.08	0.05	-10.25	0.10	0.08	ts	O.T.	-	year	-12.40	1.0332	-	14.6	-	-	-	-	-	-	-
		R 12.12.06	o73	1	5.0	-5.83	0.10	0.05	-8.74	0.12	0.08	w	3 w.	9.8	sampl.	-12.21	1.0345	2.69	9.1	sampl.	0.197	0.00475	0.0242	0.00496	0.00093	0.187
			o122	1	2.8	-4.71	0.14	0.10	-8.53	0.13	0.12	w	3 w.	9.8	sampl.	-12.21	1.0348	2.91	8.2	sampl.	0.197	0.00590	0.0300	0.00496	0.00089	0.180
			o74	1	7.6	-6.96	0.04	0.05	-10.45	0.08	0.08	ts	O.T.	-	year	-12.40	1.0330	-	15.4	-	-	-	-	-	-	-
		T 01.16.07	o75	1	6.2	-6.71	0.12	0.05	-8.31	0.08	0.08	w	3 w.	7.5	sampl.	-12.23	1.0350	2.65	7.2	sampl.	0.204	0.00405	0.0199	0.00490	0.00095	0.195
			o76	1	9.5	-7.44	0.07	0.05	-10.15	0.16	0.08	s	O.T.	-	year	-12.40	1.0333	-	14.1	-	-	-	-	-	-	-
			o77	1	11.1	-7.55	0.08	0.05	-10.25	0.10	0.08	s	O.T.	-	year	-12.40	1.0332	-	14.6	-	-	-	-	-	-	-
		V 02.20.07	o78	1	8.0	-7.52	0.04	0.05	-8.68	0.08	0.08	w	O.T.	-	year	-12.40	1.0348	-	8.0	-	-	-	-	-	-	-
			o123	1	12.3	-8.04	0.04	0.05	-10.27	0.08	0.08	s	O.T.	-	year	-12.40	1.0331	-	14.6	sampl.	-	0.00413	-	-	0.00094	-
			o79	1	7.1	-7.29	0.11	0.05	-8.18	0.10	0.08	w	3 w.	6.2	sampl.	-12.17	1.0351	2.39	6.9	sampl.	0.220	0.00357	0.0162	0.00481	0.00091	0.189
			o124	1	12.3	-6.55	0.05	0.05	-8.95	0.07	0.08	w	O.T.	-	year	-12.40	1.0345	-	9.1	sampl.	-	0.00464	-	-	0.00094	-
		Z 04.25.07	o80	1	7.5	-6.87	0.05	0.05	-10.59	0.09	0.08	ts	O.T.	-	sampl.	-12.31	1.0327	-	16.4	-	-	-	-	-	-	-

Table AII.9. *Herpetocypris reptans*

13	A-1	B	04.19.06	o93	2	3.8	-7.70	0.13	0.09	-8.39	0.11	0.14	2 w.	6.3	sampl.	-12.54	1.0352	2.58	6.3	sampl.	0.212	0.00508	0.0239	0.00461	0.00100	0.216
				o94	2	5.0	-6.40	0.07	0.12	-8.32	0.13	0.10	2 w.	6.3	sampl.	-12.54	1.0353	2.65	6.0	sampl.	0.212	0.00452	0.0213	0.00461	0.00100	0.216
				o95	2	5.7	-8.05	0.12	0.04	-7.87	0.18	0.08	2 w.	6.3	sampl.	-12.54	1.0358	3.12	4.2	sampl.	0.212	0.00488	0.0230	0.00461	0.00100	0.217
				o96	2	5.7	-7.26	0.12	0.04	-8.29	0.09	0.08	2 w.	6.3	sampl.	-12.54	1.0354	2.69	5.8	sampl.	0.212	0.00445	0.0210	0.00461	0.00108	0.234
		D	05.16.06	o97	2	2.7	-6.50	0.26	0.10	-8.14	0.19	0.15	2 w.	7.8	sampl.	-12.45	1.0354	3.12	5.6	sampl.	0.210	0.00330	0.0157	0.00398	0.00091	0.228
		J	08.10.06	o98	2	4.8	-5.88	0.09	0.12	-9.60	0.14	0.10	2 w.	14.2	sampl.	-12.30	1.0337	2.89	12.2	sampl.	0.243	0.00457	0.0189	0.00486	0.00099	0.204
				o99	2	4.9	-5.90	0.15	0.12	-9.69	0.12	0.10	2 w.	14.2	sampl.	-12.30	1.0336	2.81	12.6	sampl.	0.243	0.00416	0.0172	0.00486	0.00102	0.209
				o100	1	3.2	-5.59	0.09	0.09	-9.88	0.21	0.14	2 w.	14.2	sampl.	-12.30	1.0334	2.60	13.4	sampl.	-	-	-	0.00486	0.00101	0.207
				o101	2	5.0	-6.21	0.09	0.12	-9.53	0.12	0.10	2 w.	14.2	sampl.	-12.30	1.0338	2.97	11.9	sampl.	0.243	0.00527	0.0217	0.00486	0.00095	0.195
				o102	2	6.3	-6.14	0.09	0.04	-9.57	0.07	0.08	2 w.	14.2	sampl.	-12.30	1.0338	2.93	12.1	sampl.	0.243	0.00564	0.0233	0.00486	0.00094	0.193
				o103	2	5.1	-5.65	0.09	0.04	-9.85	0.10	0.08	2 w.	14.2	sampl.	-12.30	1.0335	2.64	13.3	sampl.	0.243	0.00482	0.0199	0.00486	0.00099	0.203
		L	09.12.06	o104	2	3.5	-6.61	0.16	0.09	-9.94	0.11	0.14	2 w.	15.6	sampl.	-12.28	1.0334	2.83	13.8	sampl.	-	-	-	0.00392	0.00102	0.260
		P	11.15.06	o105	2	5.8	-5.41	0.11	0.04	-9.92	0.10	0.08	2 w.	13.2	sampl.	-12.26	1.0334	2.30	13.8	sampl.	0.208	0.00619	0.0298	0.00495	0.00108	0.217
				o106	2	5.4	-6.04	0.10	0.04	-9.48	0.11	0.08	2 w.	13.2	sampl.	-12.26	1.0338	2.75	11.9	sampl.	0.208	0.00640	0.0308	0.00495	0.00109	0.220
		R	12.12.06	o107	2	5.7	-6.43	0.10	0.04	-9.28	0.13	0.08	2 w.	9.8	sampl.	-12.21	1.0340	2.15	11.3	sampl.	0.197	0.00595	0.0303	0.00496	0.00105	0.211
		V	02.20.07	o108	2	5.1	-7.33	0.10	0.04	-8.79	0.10	0.08	O.T.	-	dec. 06	-12.21	1.0345	-	9.3	sampl.	-	0.00476	-	-	0.00098	-
				o109	2	5.3	-7.24	0.11	0.04	-8.15	0.10	0.08	2 w.	6.2	sampl.	-12.17	1.0351	2.45	6.8	sampl.	0.220	0.00474	0.0215	0.00481	0.00088	0.183
				o110	2	4.5	-7.19	0.10	0.12	-8.88	0.11	0.10	O.T.	-	dec. 06	-12.21	1.0344	-	9.6	sampl.	-	0.00440	-	-	0.00090	-
				o111	2	5.7	-7.03	0.13	0.04	-8.72	0.15	0.08	O.T.	-	dec. 06	-12.21	1.0346	-	9.0	sampl.	-	0.00456	-	-	0.00094	-
	A-2	A	04.07.06	o128	2	2.7	-7.22	0.15	0.10	-7.79	0.11	0.11	3 w.	5.2	sampl.	-12.51	1.0358	2.92	4.9	sampl.	0.210	0.00597	0.0284	0.00451	0.00093	0.207
		B	04.19.06	o129	2	1.8	-5.48	0.15	0.18	-7.57	0.25	0.10	3 w.	6.0	sampl.	-12.54	1.0361	3.36	3.8	sampl.	-	-	-	0.00461	0.00083	0.181
		H	07.11.06	o130	2	2.1	-4.86	0.14	0.10	-9.30	0.17	0.11	3 w.	13.1	sampl.	-12.39	1.0341	3.06	11.8	sampl.	-	-	-	0.00419	0.00099	0.236
				o131	6	0.7	-5.94	0.10	0.06	-9.61	0.08	0.08	3 w.	13.1	sampl.	-12.39	1.0338	2.74	13.2	sampl.	0.208	0.00516	0.0247	0.00419	0.00113	0.271
				o132	6	2.6	-5.87	0.07	0.06	-9.64	0.12	0.10	3 w.	13.1	sampl.	-12.39	1.0338	2.71	13.3	sampl.	0.208	0.00488	0.0234	0.00419	0.00112	0.267
		R	12.12.06	o133	2	6.0	-7.69	0.45	0.20	-8.90	0.45	0.22	3 w.	9.8	sampl.	-12.21	1.0344	2.53	10.9	sampl.	-	-	-	0.00496	0.00109	0.220
		X	03.27.07	o134	2	5.8	-6.25	0.20	0.10	-8.00	0.17	0.11	3 w.	6.8	sampl.	-12.23	1.0353	2.79	6.9	-	-	-	-	-	-	-
6	Ad	A	04.07.06	o38	1	12.2	-4.83	0.04	0.05	-9.81	0.06	0.08	O.T.	-	year	-12.40	1.0336	-	12.7	-	-	-	-	-	-	-
		C	04.25.06	o39	1	12.4	-4.87	0.04	0.05	-10.97	0.05	0.08	O.T.	-	year	-12.40	1.0324	-	17.7	-	-	-	-	-	-	-
				o40	1	12.5	-3.76	0.07	0.05	-11.15	0.07	0.08	O.T.	-	year	-12.40	1.0322	-	18.5	-	-	-	-	-	-	-
				o41	1	11.7	-4.97	0.06	0.05	-10.82	0.08	0.08	O.T.	-	year	-12.40	1.0326	-	17.0	-	-	-	-	-	-	-
		I	07.24.06	o42	1	11.1	-3.75	0.05	0.05	-11.92	0.09	0.08	3 w.	23.4	sampl.	-11.94	1.0309	2.11	24.0	sampl.	0.265	0.00606	0.0229	0.00561	0.00151	0.269
		O	10.25.06	o43	1	13.4	-4.76	0.04	0.05	-10.90	0.06	0.08	3 w.	15.7	sampl.	-12.56	1.0326	2.15	16.7	sampl.	0.214	0.00553	0.0258	0.00500	0.00122	0.245
				o44	1	2.9	-5.12	0.15	0.10	-9.78	0.13	0.20										0.00525			0.00112	
				o45	1	13.1	-5.29	0.05	0.05	-10.38	0.09	0.08	3 w.	15.7	sampl.	-12.56	1.0332	2.69	14.5	sampl.	0.214	0.00579	0.0270	0.00500	0.00110	0.221
				o46	1	12.1	-5.31	0.05	0.05	-10.77	0.08	0.08	3 w.	15.7	sampl.	-12.56	1.0328	2.29	16.1	sampl.	0.214	0.00611	0.0285	0.00500	0.00119	0.238
				o47	1	10.9	-4.39	0.06	0.05	-10.19	0.08	0.08	3 w.	15.7	sampl.	-12.56	1.0334	2.89	13.7	sampl.	0.214	0.00447	0.0209	0.00500	0.00108	0.216
				o48	1	12.4	-3.63	0.08	0.05	-11.06	0.08	0.08	O.T.	-	year	-12.40	1.0323	-	18.1	-	-	-	-	-	-	-
				o49	1	15.0	-4.02	0.06	0.05	-10.99	0.06	0.08	O.T.	-	year	-12.40	1.0324	-	17.8	-	-	-	-	-	-	-
		S	01.09.07	o50	1	15.6	-4.54	0.04	0.05	-11.06	0.08	0.08	O.T.	-	year	-12.40	1.0323	-	18.1	-	-	-	-	-	-	-
				o51	1	13.2	-4.89	0.05	0.05	-10.79	0.06	0.08	O.T.	-	year	-12.40	1.0326	-	16.9	-	-	-	-	-	-	-
		U	02.15.07	o52	1	14.5	-5.07	0.04	0.05	-11.09	0.06	0.08	O.T.	-	year	-12.40	1.0323	-	18.2	-	-	-	-	-	-	-
		Y	04.10.07	o53	1	12.3	-4.72	0.06	0.05	-10.17	0.05	0.08	O.T.	-	year	-12.40	1.0332	-	14.2	-	-	-	-	-	-	-
				o54	1	12.6	-5.93	0.06	0.05	-10.01	0.08	0.08	O.T.	-	year	-12.40	1.0334	-	13.5	-	-	-	-	-	-	-
		aa	05.01.07	o55	1	10.5	-5.65	0.07	0.05	-9.94	0.04	0.08	O.T.	-	year	-11.40	1.0324	-	17.5	sampl.		0.00563			0.00112	
	A-1	O	10.25.06	o90	2	5.0	-4.83	0.10	0.12	-10.32	0.20	0.10	2 w.	16.5	1 m.	-12.42	1.0331	2.79	14.8	sampl.	0.214	0.00359	0.0168	0.00500	0.00126	0.252
				o91	2	3.7	-3.55	0.14	0.09	-9.78	0.20	0.14	2 w.	16.5	1 m.	-12.42	1.0337	3.35	12.5	sampl.	0.214	0.00478	0.0223	0.00500	0.00115	0.229
				o92	2	5.1	-4.26	0.09	0.04	-10.06	0.13	0.08	2 w.	16.5	1 m.	-12.42	1.0334	3.07	13.7	sampl.	0.214	0.00487	0.0227	0.00500	0.00120	0.239
	A-2	aa	05.01.07	o127	2	2.2	-3.20	0.18	0.10	-9.08	0.19	0.11	3 w.	13.1	sampl.	-12.08	1.0340	2.98	12.2	sampl.	-	-	-	0.00432	0.00147	0.339
3	Ad	O	10.25.06	o29	1	11.4	-4.31	0.06	0.05	-10.28	0.08	0.07	3 w.	15.9	sampl.	-12.29	1.0330	2.56	15.2	sampl.	0.227	0.00602	0.0265	0.00500	0.00109	0.219
		S	01.09.07	o30	1	12.4	-3.86	0.04	0.05	-10.78	0.08	0.07	O.T.	-	year	-12.4	1.0326	-	16.8	-	-	-	-	-	-	-
				o31	1	13.8	-3.80	0.04	0.05	-10.18	0.06	0.07	O.T.	-	year	-12.4	1.0332	-	14.2	-	-	-	-	-	-	-
				o32	1	14.2	-3.57	0.03	0.05	-9.75	0.04	0.07	O.T.	-	year	-12.4	1.0337	-	12.4	-	-	-	-	-	-	-
		U	02.15.07	o33	1	14.4	-3.25	0.05	0.05	-10.77	0.07	0.07	O.T.	-	year	-12.40	1.0326	-	16.8	-	-	-	-	-	-	-
		W	03.12.07	o34	1	12.7	-4.04	0.07	0.05	-10.84	0.06	0.07	O.T.	-	year	-12.40	1.0325	-	17.1	-	-	-	-	-	-	-
				o35	1	13.6	-4.24	0.04	0.05	-10.14	0.08	0.07	O.T.	-	year	-12.40	1.0333	-	14.1	-	-	-	-	-	-	-
		aa	05.01.07	o36	1	13.7	-3.29	0.07	0.05	-10.94	0.07	0.07	O.T.	-	year	-11.40	1.0314	-	22.0	sampl.	-	0.00638	-	-	0.00123	-
				o37	1	13.5	-4.55	0.05	0.05	-10.22	0.04	0.07	O.T.	-	year	-10.40	1.0311	-	23.2	sampl.	-	0.00620	-	-	0.00120	-
	A-1	G	06.19.06	o89	2	4.4	-3.42	0.12	0.12	-10.72	0.16	0.10	2 w.	17.2	sampl.	-12.35	1.0326	2.46	18.4	sampl.	0.232	0.00411	0.0177	0.00489	0.00117	0.240
	A-2	Q	11.28.06	o125	2	2.2	-2.81	0.10	0.10	-8.89	0.13	0.11	3 w.	11.6	sampl.	-12.21	1.0344	2.96	10.8	sampl.	-	-	-	0.00496	0.00129	0.261
		S	01.09.07	o126	1	1.2	-4.32	0.23	0.20	-8.02	0.32	0.22	3 w.	7.2	sampl.	-12.22908	1.0353	2.86	7	sampl.	-	-	-	0.00495	0.00115	0.232

Table A2.9. *Herpetocypris reptans*

Monthly averages																		
13	Ad	A	04.07.06	-7.74	-8.22	3 w.	5.2	sampl.	-12.51	1.0354		5.7		0.210	0.00451	0.0215	0.00451	0.00093	0.205
		B	04.19.06	-7.76	-8.32	3 w.	6.0	sampl.	-12.54	1.0353		6.0		0.212	0.00530	0.0249	0.00461	0.00099	0.214
		L	09.12.06	-7.08	-10.24	3 w.	14.9	sampl.	-12.28	1.0330		15.1		0.242	0.00525	0.0217	0.00392	0.00105	0.268
		N	10.10.06	-7.42	-10.43	3 w.	14.6	sampl.	-12.38	1.0330		15.4		0.227	0.00593	0.0262	0.00425	0.00108	0.253
		R	12.12.06	-5.27	-8.64	3 w.	9.8	sampl.	-12.21	1.0346		8.6		0.197	0.00533	0.0271	0.00496	0.00091	0.184
		T	01.16.07	-6.71	-8.31	3 w.	7.5	sampl.	-12.23	1.0350		7.2		0.204	0.00405	0.0199	0.00490	0.00095	0.195
		V	02.20.07	-7.29	-8.18	3 w.	6.2	sampl.	-12.17	1.0351		6.9		0.220	0.00357	0.0162	0.00481	0.00091	0.189
	A-1	B	04.19.06	-7.35	-8.22	2 w.	6.3	sampl.	-12.54	1.0354	2.76	5.6	sampl.	0.212	0.00473	0.0223	0.00461	0.00102	0.221
		D	05.16.06	-6.50	-8.14	2 w.	7.8	sampl.	-12.45	1.0354	3.12	5.6	sampl.	0.210	0.00330	0.0157	0.00398	0.00091	0.228
		J	08.10.06	-5.90	-9.69	2 w.	14.2	sampl.	-12.30	1.0336	2.81	12.6	sampl.	0.243	0.00489	0.0202	0.00486	0.00098	0.202
		L	09.12.06	-6.61	-9.94	2 w.	15.6	sampl.	-12.28	1.0334	2.83	13.8	sampl.	-	-	-	0.00392	0.00102	0.260
		P	11.15.06	-5.72	-9.70	2 w.	13.2	sampl.	-12.26	1.0336	2.53	12.8	sampl.	0.208	0.00630	0.0303	0.00495	0.00108	0.219
		R	12.12.06	-6.43	-9.28	2 w.	9.8	sampl.	-12.21	1.0340	2.15	11.3	sampl.	0.197	0.00595	0.0303	0.00496	0.00105	0.211
		V	02.20.07	-7.24	-8.15	2 w.	6.2	sampl.	-12.17	1.0351	2.45	6.8	sampl.	0.220	0.00474	0.0215	0.00481	0.00088	0.183
	A-2	A	04.07.06	-7.22	-7.79	3 w.	5.2	sampl.	-12.51	1.0358	2.92	4.9	sampl.	0.210	0.00597	0.0284	0.00451	0.00093	0.207
		B	04.19.06	-5.48	-7.57	3 w.	6.0	sampl.	-12.54	1.0361	3.36	3.8	-	-	-	-	-	-	-
		H	07.11.06	-5.56	-9.52	3 w.	13.1	sampl.	-12.39	1.0339	2.83	12.8	sampl.	0.208	0.00502	0.0241	0.00419	0.00108	0.258
		R	12.12.06	-7.69	-8.90	3 w.	9.8	sampl.	-12.21	1.0344	2.53	10.9	sampl.	-	-	-	0.00496	0.00109	0.220
		X	03.27.07	-6.25	-8.00	3 w.	6.8	sampl.	-12.23	1.0353	2.79	6.9	-	-	-	-	-	-	-
6	Ad	I	07.24.06	-3.75	-11.92	3 w.	23.4	sampl.	-11.94	1.0309		24.0		0.265	0.00606	0.0229	0.00561	0.00151	0.269
		O	10.25.06	-4.94	-10.56	3 w.	15.7	smpl.	-12.56	1.0330		15.2		0.214	0.00548	0.0256	0.00500	0.00115	0.230
	A-1	O	10.25.06	-4.21	-10.05	2 w.	16.5	1 m.	-12.42	1.0334	3.07	13.6	sampl.	0.214	0.00441	0.0206	0.00500	0.00120	0.240
	A-2	aa	05.01.07	-3.20	-9.08	3 w.	13.1	sampl.	-12.08	1.0340	2.98	12.2	sampl.	-	-	-	0.00432	-	0.339
3	Ad	O	10.25.06	-4.31	-10.28	3 w.	15.9	sampl.	-12.29	1.0330		15.2		0.227	0.00602	0.0265	0.00500	0.00109	0.219
	A-1	G	06.19.06	-3.42	-10.72	2 w.	17.2	sampl.	-12.35	1.0326	2.46	18.4	sampl.	0.232	0.00411	0.0177	0.00489	0.00117	0.240
	A-2	Q	11.28.06	-2.81	-8.89	3 w.	11.6	sampl.	-12.21	1.0344	2.96	10.8	sampl.	-	-	-	0.00496	-	0.261
	A-2	S	01.09.07	-4.32	-8.02	3 w.	7.2	sampl.	-12.23	1.0353	2.86	7.0	sampl.	-	-	-	0.00495	-	0.232

TABLE AII.10
Geochemical composition of *Isocypris beauchampi.*

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
33	Ad	G	06.19.06	o651	2	0.5	-7.14	0.38	0.54	-7.84	0.70	0.29	4 m.	5.8	2 m.	-12.46	1.0357	2.97	5.5	1 m.	-	-	-	-	-	-
		S	01.09.07	o652	2	1.1	-6.95	0.34	0.22	-8.68	0.46	0.07	4 m.	7.9	2 m.	-12.38	1.0348	2.50	8.5	1 m.	-	-	-	0.00502	0.00141	0.281
13	Ad	P	11.15.06	o648	2	1.1	-6.57	0.31	0.22	-10.27	0.44	0.07	4 m.	14.4	2 m.	-12.28	1.0330	2.23	14.3	1 m.	-	-	-	0.00425	0.00126	0.297
		V	02.20.07	o649	5	2.6	-6.79	0.27	0.06	-8.58	0.17	0.07	4 m.	9.2	2 m.	-12.21	1.0347	2.71	8.8	1 m.	-	-	-	0.00490	0.00126	0.256
		X	03.27.07	o650	3	1.5	-6.81	0.22	0.22	-8.23	0.23	0.07	4 m.	7.4	2 m.	-12.23	1.0351	2.69	7.5	1 m.	-	-	-	0.00481	0.00124	0.258

TABLE AII.11
Geochemical composition of *Cypridopsis vidua.*

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
3	Ad	G	06.19.06	o186	20	8.0	-2.82	0.08	0.07	-11.12	0.09	0.08	1 w.	18.3	sampl.	-12.35	1.0322	3.44	18.7	sampl.	0.232	0.0082	0.035	0.00489	0.00128	0.262
		I	07.24.06	o187	20	12.1	-3.01	0.07	0.07	-12.38	0.07	0.08	1 w.	25.9	sampl.	-11.91	1.0304	2.73	25.3	sampl.	0.279	0.0110	0.04	0.00575	0.00170	0.295
		K	08.31.06	o188	20	9.1	-2.86	0.10	0.07	-11.54	0.10	0.08	O.T.	-	year	-12.40	1.0318	3.35	20.1	-	-	-	-	-	-	-
		M	10.04.06	o189	20	9.5	-3.35	0.05	0.07	-11.13	0.09	0.08	1 w.	18.3	sampl.	-12.44	1.0323	3.71	18.4	sampl.	0.225	0.0088	0.039	0.00511	0.00129	0.253
		O	10.25.06	o190	20	9.2	-3.18	0.06	0.07	-11.13	0.09	0.08	O.T.	-	year	-12.40	1.0322	-	18.5	-	-	-	-	-	-	-
				o191	20	9.2	-3.63	0.09	0.07	-10.81	0.12	0.08	O.T.	-	year	-12.40	1.0326	3.15	17.3	-	-	-	-	-	-	-
		Q	11.28.06	o192	12	5.6	-3.00	0.09	0.08	-11.06	0.11	0.08	O.T.	-	year	-12.40	1.0323	-	18.2	-	-	-	-	-	-	-
		S	01.09.07	o193	20	10.0	-3.26	0.09	0.07	-10.67	0.05	0.08	O.T.	-	year	-12.40	1.0327	2.68	16.8	-	-	-	-	-	-	-
		W	03.12.07	o194	20	8.7	-3.45	0.08	0.07	-10.91	0.09	0.08	O.T.	-	year	-12.40	1.0325	-	17.7	-	-	-	-	-	-	-
		Y	04.10.07	o195	6	3.2	-2.94	0.14	0.08	-10.39	0.24	0.11	O.T.	-	year	-12.40	1.0330	-	15.8	-	-	-	-	-	-	-
		aa	05.01.07	o196	19	9.2	-3.66	0.08	0.07	-10.68	0.11	0.08	O.T.	-	year	-12.40	1.0327	3.19	16.8	-	-	-	-	-	-	-
	A-1	E	05.24.06	o185	7	0.7	-3.73	0.31	0.10	-8.40	0.47	0.29	1 d	9.0	sampl.	-12.42	1.0351	-	8.5	sampl.		-	-	0.00473	0.00125	0.264
6	Ad	I	07.24.06	o198	20	10.4	-2.93	0.05	0.04	-12.17	0.09	0.08	1 w.	24.3	sampl.	-11.94	1.0307	-	24.3	sampl.	0.265	0.0103	0.039	0.00561	0.00159	0.283
		K	08.31.06	o199	20	9.1	-4.47	0.06	0.04	-11.46	0.07	0.08	O.T.	-	year	-12.40	1.0319	-	19.8	-	-	-	-	-	-	-
		M	10.04.06	o200	20	9.8	-3.85	0.05	0.04	-11.21	0.07	0.08	1 w.	17.9	sampl.	-12.42	1.0322	3.24	18.7	sampl.	0.223	0.0090	0.0401	0.00493	0.00131	0.241
		O	10.25.06	o201	26	11.7	-4.29	0.05	0.04	-10.97	0.09	0.08	O.T.	-	year	-12.40	1.0324	3.23	17.9	-	-	-	-	-	-	-
				o203	11	5.2	-4.46	0.07	0.04	-10.94	0.15	0.14	O.T.	-	year	-12.40	1.0324	3.49	17.8	-	-	-	-	-	-	-
		Q	11.28.06	o202	24	10.0	-4.34	0.06	0.04	-10.78	0.08	0.08	O.T.	-	year	-12.40	1.0326	3.42	17.2	-	-	-	-	-	-	-
		S	01.09.07	o204	11	4.6	-4.39	0.09	0.04	-10.83	0.11	0.14	O.T.	-	year	-12.40	1.0326	3.63	17.4	-	-	-	-	-	-	-

TABLE AII.12
Geochemical composition of *Plesiocypridopsis newtoni.*

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
6	Ad	M	10.04.06	o646	2	1.0	-3.67	0.34	0.23	-11.27	0.42	0.16	1 w.	17.9	sampl.	-12.42	1.0321	2.12	18.2	-	-	-	-	-	-	-
3	Ad	I	07.24.06	o644	2	1.0	-2.88	0.40	0.23	-12.27	0.51	0.16	1 w.	25.9	sampl.	-11.91	1.0305	2.25	25.3	-	-	-	-	-	-	-
		M	10.04.06	o645	8	3.2	-3.80	0.19	0.18	-11.23	0.17	0.05	1 w.	18.3	sampl.	-12.44	1.0322	2.26	17.9	sampl.	-	-	-	0.00511	0.00121	0.236

TABLE AII.13
Geochemical composition of *Potamocypris similis*.

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
3	Ad	G	06.19.06	o636	9	2.7	-3.56	0.15	0.31	-11.12	0.25	0.14	1 w.	18.3	sampl.	-12.35	1.0322	2.29	17.8	sampl.	-	-	-	0.00489	0.00148	0.303
		I	07.24.06	o637	10	3.2	-2.53	0.15	0.18	-12.64	0.15	0.05	1 w.	25.9	sampl.	-11.91	1.0302	1.87	27.1	sampl.	0.279	0.00503	0.0180	0.00575	0.00210	0.365
		O	10.25.06	o638	10	2.8	-3.07	0.12	0.31	-10.84	0.43	0.14	1 w.	16.4	sampl.	-12.29	1.0324	2.09	16.8	sampl.	-	-	-	0.00500	0.00149	0.299

TABLE AII.14
Geochemical composition of *Potamocypris smaragdina.*

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
6	Ad	K	08.31.06	o640	8	1.6	-4.41	0.26	0.23	-10.93	0.20	0.16	1 w.	15.8	sampl.	-12.37	1.0324	1.96	16.8	-	-	-	-	-	-	-
		M	10.04.06	o641	5	1.0	-4.17	0.36	0.23	-11.03	0.44	0.16	1 w.	17.9	sampl.	-12.42	1.0324	2.36	17.1	-	-	-	-	-	-	-
		O	10.25.06	o643	4	0.8	-4.80	0.45	0.23	-11.05	0.52	0.16	1 w.	16.3	sampl.	-12.56	1.0325	2.14	16.5	-	-	-	-	-	-	-
		Q	11.28.06	o642	4	0.8	-4.72	0.43	0.23	-10.63	0.65	0.16	O.T.	-	sampl.	-12.22	1.0326	-	16.2	-	-	-	-	-	-	-
3	Ad	M	10.04.06	o639	8	1.6	-3.72	0.27	0.23	-11.16	0.31	0.16	1 w.	18.3	sampl.	-12.44	1.0323	2.34	17.6	sampl.	-	-	-	0.00511	0.00154	0.301

TABLE AII.15
Geochemical composition of *Limnocythere inopinata*.

depth	age & sex	sampling	ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)					(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
13	Ad	H 07.11.06	o352	11	2.7	-8.23	0.15	0.21	-10.49	0.19	0.14	2 w.	13.5	sampl.	-12.39	1.0329	1.92	12.3	sampl.	-	-	-	0.00419	0.00139	0.331
		J 08.10.06	o353	15	2.6	-8.02	0.15	0.21	-10.69	0.18	0.14	2 w.	14.2	sampl.	-12.30	1.0326	1.77	13.7	sampl.	-	-	-	0.00486	0.00127	0.260
6	Ad	E 05.24.06	o359	30	8.7	-7.03	0.07	0.08	-10.12	0.09	0.07	2 w.	9.2	sampl.	-12.42	1.0333	1.36	10.6	sampl.	0.219	0.00269	0.0068	0.00458	0.00150	0.327
		G 06.19.06	o360	33	8.1	-6.95	0.06	0.08	-11.00	0.07	0.07	2 w.	15.5	sampl.	-12.36	1.0323	1.81	14.8	sampl.	0.234	0.00229	0.0064	0.00466	0.00151	0.323
		I 07.24.06	o361	30	8.4	-6.20	0.11	0.08	-12.62	0.10	0.07	2 w.	23.5	sampl.	-11.94	1.0302	1.41	24.3	sampl.	0.265	0.00239	0.0062	0.00561	0.00164	0.293
		O 10.25.06	o362	18	4.4	-6.47	0.09	0.08	-11.30	0.15	0.07	2 w.	16.5	sampl.	-12.56	1.0322	1.93	15.3	sampl.		-	-	0.00500	0.00154	0.307
		aa 05.01.07	o363	8	0.8	-7.50	0.42	0.11	-10.61	0.41	0.07	2 w.	14.2	sampl.	-12.08	1.0324	1.63	14.3	-	-	-	-	-	-	-
3	Ad	E 05.24.06	o354	39	9.7	-6.45	0.08	0.10	-10.25	0.07	0.06	2 w.	11.0	sampl.	-12.42	1.0332	1.63	11.2	sampl.	0.221	0.00227	0.0064	0.00473	0.00141	0.299
		G 06.19.06	o355	17	4.2	-6.14	0.13	0.10	-11.65	0.09	0.06	2 w.	17.2	sampl.	-12.35	1.0317	1.50	17.8	sampl.	0.232	0.00367	0.0064	0.00489	0.00149	0.305
		K 08.31.06	o357	37	7.2	-5.34	0.05	0.10	-11.72	0.14	0.06	2 w.	17.5	sampl.	-12.38	1.0316	1.52	18.0	sampl.	0.232	0.00232	0.0069	0.00486	0.00160	0.329
		O 10.25.06	o358	9	2.1	-5.41	0.16	0.21	-11.32	0.20	0.14	2 w.	16.6	sampl.	-12.29	1.0319	1.63	16.6	sampl.	-	-	-	0.00500	0.00143	0.286
		I 07.24.06	o356*	33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE AII.16
Geochemical composition of *Limnocytherina sanctipatricii.*

depth	age & sex	sampling	ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)					(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
13	Adf	B 04.19.06	o368	4	2.1	-7.90	0.18	0.11	-8.74	0.17	0.07	1 m.	5.8	1 m.	-12.51	1.0348	2.06	4.8	1 m.	-	-	-	0.00451	0.00169	0.374
	Adf	H 07.11.06	o369	2	1.1	-7.27	0.36	0.11	-10.42	0.25	0.07	1 m.	12.7	1 m.	-12.40	1.0330	1.83	12.7	1 m.	-	-	-	0.00430	(0.00197)	(0.456)
	Adm	B 04.19.06	o364	10	4.0	-9.13	0.12	0.08	-9.18	0.12	0.07	1 m.	5.8	1 m.	-12.51	1.0344	1.61	6.7	1 m.	-	-	-	0.00451	0.00164	0.363
	Adm	Z 04.25.07	o367	2	1.1	-8.17	0.35	0.11	-9.22	0.26	0.07	1 m.	8.1	1 m.	-12.23	1.0341	1.83	8.0	1 m.	-	-	-	0.00484	(0.00178)	(0.367)
	Ad	D+F	o365	8	3.7	-7.75	0.13	0.08	-9.64	0.27	0.07	1 m.	8.8	1 m.	-12.49	1.0339	1.84	8.8	1 m.	-	-	-	0.00430	0.00170	0.395
	Ad	V+X	o366	6	2.3	-7.87	0.18	0.11	-8.97	0.14	0.07	1 m.	6.5	1 m.	-12.28	1.0344	1.77	6.7	1 m.	-	-	-	0.00486	0.00185	0.381
	A-1	B+V+X	o370	3	1.5	-8.36	0.26	0.11	-9.01	0.32	0.07	1 w.	6.5	sampl	-12.39	1.0344	1.84	6.5	sampl.	-	-	-	0.00476	0.00162	0.341
	A-1	F+Z	o371	2	1.7	-7.99	0.12	0.11	-10.10	0.18	0.07	1 w.	11.4	sampl.	-12.35	1.0333	1.81	11.4	sampl.	-	-	-	0.00465	0.00189	0.405

TABLE AII.17
Geochemical composition of *Cytherissa lacustris*.

depth	age & sex	sampling		ananlyse identifier	nbr. of vavles	area 44/45/46	$\delta^{13}C_{ostra}$	int. std.	ext. std.	$\delta^{18}O_{ostra}$	int. std.	ext. std.	mean period for T_c	T_c	date $\delta^{18}O_{H2O}$	$\delta^{18}O_{H2O}$	$\alpha_{calcite-water}$	vital effect	$\delta^{18}O$ calc. T_c	date X/Ca_{H2O}	Mg/Ca_{H2O}	accepted Mg/Ca_{ostra}	D_{Mg}	Sr/Ca_{H2O}	accepted Sr/Ca_{ostra}	D_{Sr}
(m)						(mV)	(‰VPDB)			(‰VPDB)				°C		(‰VSMOW)		(‰)	(°C)	molar ratio				molar ratio		
All values																										
70	Ad	A	04.07.06	o480	2	4.5	-7.65	0.06	0.06	-8.41	0.15	0.07	3 m.	4.8	1 m.	-12.64	1.0353	2.33	4.8	sampl.	0.220	0.00346	0.016	0.00367	0.00271	0.738
		B	04.19.06	o481	2	3.7	-9.35	0.13	0.06	-7.99	0.23	0.07	3 m.	4.8	1 m.	-12.64	1.0358	2.75	3.2	sampl.	0.220	0.00477	0.022	0.00367	0.00358	0.975
				o587	2	2.6	-6.73	0.13	0.12	-7.97	0.25	0.11	3 m.	4.8	1 m.	-12.64	1.0358	2.77	3.1	1 m.	0.220	0.00506	0.0230	0.00367	0.00298	0.810
		D	05.16.06	o482	2	4.1	-7.62	0.16	0.06	-7.80	0.17	0.07	3 m.	4.8	1 m.	-12.64	1.0360	2.94	2.5	1 m.	0.220	0.00440	0.0200	0.00367	0.00300	0.817
				o483	2	4.2	-6.91	0.12	0.06	-8.13	0.15	0.07	3 m.	4.8	1 m.	-12.64	1.0356	2.61	3.7	-	-	-	-	-	-	-
		F	06.12.06	o484	2	3.3	-7.52	0.12	0.06	-7.88	0.10	0.07	3 m.	4.9	1 m.	-12.41	1.0357	2.67	3.6	-	-	-	-	-	-	-
				o485	4	7.3	-8.21	0.06	0.06	-8.19	0.07	0.07	3 m.	4.9	1 m.	-12.41	1.0353	2.35	4.8	2 m.	0.211	0.00343	0.0162	0.00371	0.00308	0.830
		H	07.11.06	o486	2	4.8	-9.67	0.15	0.06	-8.47	0.13	0.07	3 m.	5.1	1 m.	-12.58	1.0352	2.27	5.3	2 m.	0.213	0.00448	0.0210	0.00381	0.00303	0.795
		J	08.10.06	o487	2	3.6	-8.28	0.12	0.06	-7.88	0.21	0.07	3 m.	5.3	1 m.	-12.33	1.0356	2.67	4.0	2 m.	0.213	0.00457	0.0214	0.00381	0.00311	0.816
				o489	4	5.3	-8.92	0.07	0.06	-8.30	0.10	0.07	3 m.	5.3	1 m.	-12.33	1.0351	2.24	5.6	2 m.	0.213	0.00391	0.0183	0.00381	0.00307	0.807
				o488	4	5.5	-9.15	0.10	0.06	-8.69	0.08	0.07	3 m.	5.3	1 m.	-12.33	1.0347	1.84	7.1	2 m.	0.213	0.00454	0.0213	0.00381	0.00316	0.829
				o490	4	6.7	-9.71	0.06	0.06	-8.60	0.07	0.07	3 m.	5.3	1 m.	-12.33	1.0348	1.93	6.8	-	-	-	-	-	-	-
		P	11.15.06	o491	2	3.7	-7.66	0.11	0.06	-8.14	0.16	0.07	3 m.	5.7	1 m.	-12.34	1.0353	2.50	4.9	-	-	-	-	-	-	-
		R	12.12.06	o588	2	1.8	-8.67	0.13	1.92	-8.25	0.29	0.19	3 m.	5.7	1 m.	-12.29	1.0351	2.35	5.6	-	-	-	-	-	-	-
		T	01.16.07	o492	2	3.6	-7.70	0.14	0.06	-8.25	0.18	0.07	3 m.	5.7	1 m.	-12.28	1.0351	2.32	5.6	-	-	-	-	-	-	-
		V	02.20.07	o493	2	3.9	-7.86	0.12	0.06	-8.18	0.10	0.07	3 m.	5.7	1 m.	-12.21	1.0351	2.32	5.6	2 m.	0.212	0.00376	0.0177	0.00375	0.00300	0.799
				o494	2	3.7	-8.97	0.10	0.06	-8.20	0.13	0.07	3 m.	5.7	1 m.	-12.21	1.0351	2.30	5.7	2 m.	0.214	0.00486	0.0227	0.00454	0.00295	0.650
		X	03.27.07	o495	2	3.7	-7.15	0.08	0.06	-8.12	0.19	0.07	3 m.	5.9	1 m.	-12.33	1.0353	2.56	4.9	3 m.	-	-	-	0.00454	0.00373	0.820
				o589	2	2.2	-7.86	0.20	0.12	-8.18	0.18	0.11	3 m.	5.9	1 m.	-12.33	1.0353	2.50	5.1	-	-	-	-	-	-	-
	A-1	H	07.11.06	o597	4	2.0	-8.45	0.12	0.15	-8.49	0.27	0.06	4 m.	5	1 m.	-12.58	1.0352	2.22	5.4	2 m.	0.213	0.00480	0.023	0.00381	0.00264	0.693
		J	08.10.06	o506	8	4.0	-9.63	0.21	0.11	-8.55	0.17	0.15	4 m.	5.2	1 m.	-12.33	1.0349	1.95	6.6	-	-	-	-	-	-	-
		N	10.10.06	o598	4	1.7	-8.38	0.17	0.15	-8.22	0.24	0.06	4 m.	5.53	1 m.	-12.45	1.0353	2.49	4.8	2 m.	0.212	0.00513	0.024	0.00375	0.00335	0.892
		V	02.20.07	o600	6	2.8	-8.78	0.13	0.09	-8.30	0.30	0.13	4 m.	5.7	1 m.	-12.21	1.0350	2.20	6.1	2 m.	0.214	0.00644	0.0301	0.00454	0.00324	0.714
		X	03.27.07	o601	4	2.1	-4.67	0.15	0.09	-7.79	0.28	0.13	4 m.	5.8	1 m.	-12.33	1.0357	2.88	3.6	2 m.	0.213	0.00536	0.0251	0.00355	0.00258	0.726
		Z	04.25.07	o507	13	6.4	-8.06	0.11	0.09	-7.87	0.09	0.05	4 m.	6.1	1 m.	-12.24	1.0355	2.75	4.3	-	-	-	-	-	-	-
	A-2	B	04.19.06	o622	11	2.6	-7.92	0.18	0.31	-8.14	0.32	0.14	3 m.	4.8	2 m.	-12.64	1.0356	2.59	3.8	sampl.	0.220	0.00497	0.0226	0.00367	0.00310	0.844
		D	05.16.06	o553	28	7.7	-8.71	0.04	0.07	-8.43	0.09	0.07	3 m.	4.8	2 m.	-12.64	1.0353	2.29	4.9	1 m.	0.220	0.00565	0.0257	0.00367	0.00288	0.783
		H	06.12.06	o554	19	4.5	-9.45	0.12	0.07	-8.47	0.11	0.07	3 m.	4.9	2 m.	-12.64	1.0353	2.27	5.1	2 m.	0.220	0.00569	0.0259	0.00367	0.00336	0.915
		J	07.11.06	o555	28	8.8	-8.80	0.06	0.07	-8.42	0.06	0.07	3 m.	5.1	2 m.	-12.64	1.0353	2.37	4.9	-	-	-	-	-	-	-
		L	08.10.06	o623	6	1.1	-7.33	0.70	0.23	-8.40	0.64	0.16	3 m.	5.3	2 m.	-12.41	1.0351	2.21	5.7	2 m.	-	-	-	0.00381	0.00287	0.753
		N	09.12.06	o556	28	7.8	-8.31	0.05	0.07	-8.46	0.08	0.07	3 m.	5.5	2 m.	-12.58	1.0352	2.37	5.2	-	-	-	-	-	-	-
		P	10.10.06	o557	26	6.6	-9.11	0.09	0.07	-8.58	0.09	0.07	3 m.	5.6	2 m.	-12.33	1.0348	2.02	6.7	2 m.	0.214	0.00481	0.0225	0.00424	0.00321	0.757
		R	11.15.06	o558	28	8.2	-8.45	0.05	0.07	-8.51	0.09	0.07	3 m.	5.7	2 m.	-12.39	1.0350	2.16	6.2	2 m.	0.215	0.00521	0.0242	0.00469	0.00265	0.565
		T	12.12.06	o559	22	5.4	-8.84	0.14	0.07	-8.48	0.14	0.07	3 m.	5.7	2 m.	-12.45	1.0351	2.26	5.9	2 m.	0.215	0.00465	0.0216	0.00365	0.00301	0.825
		V	01.16.07	o560	28	8.8	-8.45	0.09	0.07	-8.48	0.07	0.07	3 m.	5.7	2 m.	-12.34	1.0349	2.14	6.3	-	-	-	-	-	-	-
		X	02.20.07	o561	29	7.1	-8.53	0.07	0.07	-8.37	0.10	0.07	3 m.	5.7	2 m.	-12.29	1.0350	2.20	6.1	2 m.	0.212	0.00468	0.0220	0.00375	0.00269	0.716
		Z	04.25.07	o562	28	9.0	-8.55	0.05	0.07	-8.41	0.09	0.07	3 m.	6.2	2 m.	-12.21	1.0349	2.21	6.5	2 m.	0.213	0.00499	0.0234	0.00355	0.00273	0.767
				o563	24	6.3	-8.33	0.10	0.07	-8.43	0.13	0.07	3 m.	6.2	2 m.	-12.21	1.0349	2.19	6.6	2 m.	0.213	0.00485	0.0227	0.00355	0.00319	0.896

33	Ad	A	04.07.06	o446	4	6.7	-8.06	0.10	0.06	-8.64	0.09	0.07	O.T.	-	year	-12.40	1.0348	-	6.7	-	-	0.00519	-	-	0.00312	-
				o447	4	7.7	-8.91	0.08	0.06	-8.69	0.17	0.07	O.T.	-	year	-12.40	1.0348	-	6.9	-	-	0.00399	-	-	0.00286	-
		C	04.25.06	o578	2	3.2	-8.61	0.16	0.12	-8.96	0.21	0.11	O.T.	-	year	-12.40	1.0345	-	7.9	-	-	0.00574	-	-	0.00327	-
				o579*	2	1.5	-6.58	0.13	1.92	-7.53	0.27	0.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		G	06.19.06	o580*	2	1.3	-7.38	0.40	1.92	-8.20	0.54	0.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-
				o581	2	3.0	-8.69	0.13	0.12	-8.78	0.22	0.11	O.T.	-	year	-12.40	1.0347	-	7.2	-	-	-	-	-	-	-
		K	08.31.06	o582	2	2.7	-4.22	0.23	0.12	-8.59	0.30	0.11	O.T.	-	year	-12.40	1.0349	-	6.5	-	-	-	-	-	-	-
		O	10.25.06	o583	2	2.9	-8.44	0.11	0.12	-8.49	0.18	0.11	4 m.	7.2	1 m.	-12.31	1.0349	2.46	6.4	-	-	-	-	-	-	-
				o448	4	6.2	-7.69	0.14	0.06	-8.77	0.10	0.07	4 m.	7.6	1 m.	-12.38	1.0347	2.33	7.3	2 m.	0.216	0.00422	0.0195	0.00478	0.00297	0.621
				o449	4	7.1	-8.67	0.07	0.06	-9.04	0.14	0.07	4 m.	7.6	1 m.	-12.38	1.0344	2.05	8.4	2 m.	0.216	0.00317	0.0147	0.00478	0.00295	0.617
				o584*	4	3.6	-5.29	0.17	0.12	-8.34	0.18	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		S	01.09.07	o450	4	6.6	-7.84	0.11	0.06	-8.38	0.09	0.07	4 m.	7.9	1 m.	-12.31	1.0350	2.74	6.0	2 m.	0.216	0.00503	0.0232	0.00486	0.00255	0.525
				o451	4	7.6	-8.05	0.10	0.06	-8.65	0.10	0.07	4 m.	7.9	1 m.	-12.31	1.0347	2.46	7.0	2 m.	0.216	0.00471	0.0218	0.00486	0.00285	0.586
		U	02.15.07	o452	4	5.0	-8.68	0.13	0.06	-8.77	0.11	0.07	O.T.	-	year	-12.40	1.0347	-	-	-	-	-	-	-	-	-
		W	03.12.07	o453	4	5.6	-6.82	0.09	0.06	-8.14	0.06	0.07	O.T.	-	year	-12.40	1.0354	-	4.7	-	-	-	-	-	-	-
				o454	5	7.6	-7.93	0.10	0.06	-8.70	0.09	0.07	O.T.	-	year	-12.40	1.0348	-	6.9	-	-	-	-	-	-	-
				o585*	4	2.9	-5.92	0.14	0.12	-7.62	1.11	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Y	04.10.07	o586*	4	3.1	-3.24	0.17	0.12	-7.91	0.17	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		aa	05.01.07	o455	4	7.1	-6.15	0.08	0.06	-8.21	0.11	0.07	O.T.	-	year	-12.40	1.0353	-	5.0	-	-	-	-	-	-	-
	A-1	M	10.04.06	o501	10	5.7	-8.79	0.09	0.09	-8.76	0.12	0.05	4 m.	7.1	1 m.	-12.49	1.0348	2.34	6.8	-	-	-	-	-	-	-
		O	10.25.06	o502	11	7.1	-7.06	0.13	0.09	-8.36	0.13	0.05	4 m.	7.2	1 m.	-12.31	1.0350	2.59	5.9	2 m.	0.217	0.00559	0.0258	0.00486	0.00283	0.582
				o503	8	6.0	-8.33	0.11	0.09	-8.51	0.10	0.05	O.T.	-	year	-12.40	1.0350	-	-	-	-	-	-	-	-	-
		S	01.09.07	o595	4	1.4	-7.64	0.21	1.92	-8.75	0.22	0.19	O.T.	-	year	-12.40	1.0347	-	-	-	-	0.00538	-	-	0.00289	-
		U	02.15.07	o504	10	5.5	-6.86	0.17	0.09	-8.40	0.13	0.05	O.T.	-	year	-12.40	1.0351	-	-	-	-	0.00542	-	-	0.00305	-
		Y	04.10.07	o505	8	4.4	-6.22	0.10	0.11	-8.12	0.11	0.15	O.T.	-	year	-12.40	1.0354	-	-	-	-	0.00556	-	-	0.00247	-
		aa	05.01.07	o596	2	1.0	-9.24	0.18	0.15	-8.43	0.52	0.06	4 m.	6.6	1 m.	-12.26	1.0349	2.32	6.4	2 m.	-	-	-	0.00486	0.00319	0.658
	A-2	A	04.07.06	o614	12	3.0	-7.92	0.21	0.09	-8.71	0.16	0.13	O.T.	-	year	-12.40	1.0348		7.0	-	-	0.00574	-	-	0.00277	-
		C	04.25.06	o615	10	2.0	-7.58	0.10	0.15	-8.57	0.57	0.06	O.T.	-	year	-12.40	1.0349		6.4	-	-	0.00641	-	-	0.00301	-
		G	06.19.06	o617	9	1.5	-8.22	0.25	0.15	-8.94	0.44	0.06	O.T.	-	year	-12.40	1.0345		7.8	-	-	-	-	-	-	-
		I	07.24.06	o618	8	1.9	-7.20	0.27	0.15	-8.87	0.53	0.06	O.T.	-	year	-12.40	1.0346		7.6	-	-	0.00520	-	-	0.00318	-
		K	08.31.06	o619	13	2.9	-7.37	0.18	0.09	-8.60	0.14	0.13	O.T.	-	year	-12.40	1.0349		6.5	-	-	-	-	-	-	-
		M	10.04.06	o547	16	3.6	-8.36	0.11	0.07	-8.88	0.09	0.07	O.T.	-	year	-12.40	1.0346		7.6	-	-	-	-	-	-	-
		O	10.25.06	o620	12	3.2	-8.29	0.19	0.07	-8.82	0.12	0.05	O.T.	-	year	-12.40	1.0346		7.4	-	-	-	-	-	0.00293	-
		Q	11.28.06	o621	14	2.7	-8.56	0.22	0.31	-8.87	0.18	0.14	3 m.	7.8	2 m.	-12.49	1.0347	2.39	7.2	2 m.	0.216	0.00547	0.0254	0.00478	0.00306	0.640
		S	01.09.07	o548	28	8.7	-7.91	0.05	0.07	-8.96	0.08	0.07	3 m.	8.0	2 m.	-12.31	1.0344	2.17	8.3	2 m.	0.216	0.00579	0.0267	0.00486	0.00272	0.560
		U	02.15.07	o549	28	6.6	-7.62	0.10	0.07	-8.70	0.12	0.07	3 m.	7.3	2 m.	-12.38	1.0348	2.34	7.0	-	-	-	-	-	-	-
		W	03.12.07	o550	28	7.2	-7.36	0.06	0.07	-8.73	0.07	0.07	3 m.	6.8	2 m.	-12.31	1.0347	2.12	7.4	2 m.	0.219	0.00532	0.0243	0.00478	0.00320	0.669
		Y	04.10.07	o551	27	5.8	-7.19	0.09	0.07	-8.52	0.08	0.07	3 m.	6.4	2 m.	-12.31	1.0349	2.26	6.5	2 m.	0.218	0.00598	0.0274	0.00484	0.00320	0.660
		aa	05.01.07	o552	25	6.6	-7.61	0.06	0.07	-8.70	0.06	0.07	O.T.	-	year	-12.40	1.0348		6.9	-	-	-	-	-	-	-

Table AII.17. *Cytherissa lacustris*

13	Ad	D	05.16.06	o576*	6	1.8	-8.34	0.26	1.92	-8.72	0.24	0.19	-	-	-	-	-	-	-	-	-	-	-	-	-
		F	06.12.06	o440	4	6.5	-6.98	0.10	0.05	-9.01	0.09	0.05	3 m.	6.9	2 m.	-12.54	1.0346	2.10	7.6	2 m.	0.212	0.00514	0.0242	0.00461	0.00303	0.657
				o441	4	8.3	-7.94	0.03	0.05	-8.71	0.10	0.05	3 m.	6.9	2 m.	-12.54	1.0349	2.41	6.4	2 m.	0.212	0.00503	0.0237	0.00461	0.00340	0.738
		H	07.11.06	o442	4	5.8	-8.48	0.06	0.05	-8.60	0.08	0.05	O.T.	-	year	-12.40	1.0349	-	6.5	-	-	-	-	-	-	-
				o443	4	8.0	-8.29	0.09	0.05	-8.96	0.03	0.05	O.T.	-	year	-12.40	1.0345	-	7.9	-	-	-	-	-	-	-
				o444	4	9.4	-7.70	0.07	0.05	-8.32	0.10	0.05	O.T.	-	year	-12.40	1.0352	-	5.4	-	-	-	-	-	-	-
				o445	4	6.4	-8.28	0.09	0.05	-9.84	0.09	0.05	O.T.	-	year	-12.40	1.0336	-	11.5	-	-	-	-	-	-	-
				o571	1	1.8	-7.93	0.25	1.92	-9.52	0.30	0.19	O.T.	-	year	-12.40	1.0339	-	10.2	-	-	-	-	-	-	-
		J	08.10.06	o421	4	6.0	-7.52	0.05	0.05	-9.47	0.07	0.05	O.T.	-	year	-12.40	1.0340	-	10.0	-	-	0.00500	-	-	0.00269	-
				o422	4	6.7	-7.94	0.07	0.05	-9.53	0.13	0.05	O.T.	-	year	-12.40	1.0339	-	10.2	-	-	0.00427	-	-	0.00308	-
				o423	4	6.9	-7.90	0.05	0.05	-9.54	0.09	0.05	O.T.	-	year	-12.40	1.0339	-	10.3	-	-	0.00464	-	-	0.00265	-
				o424	4	8.1	-8.06	0.06	0.05	-9.42	0.09	0.05	O.T.	-	year	-12.40	1.0340	-	9.8	-	-	0.00453	-	-	0.00266	-
				o425	4	8.0	-8.50	0.08	0.05	-9.44	0.06	0.05	O.T.	-	year	-12.40	1.0340	-	9.9	-	-	0.00542	-	-	0.00269	-
		L	09.12.06	o426	4	6.5	-6.86	0.10	0.05	-9.18	0.11	0.05	O.T.	-	year	-12.40	1.0343	-	8.8	-	-	0.00611	-	-	0.00310	-
				o427	4	8.3	-8.08	0.06	0.05	-8.81	0.10	0.05	O.T.	-	year	-12.40	1.0347	-	7.3	-	-	0.00468	-	-	0.00253	-
				o428	4	8.1	-7.16	0.06	0.05	-9.50	0.33	0.05	O.T.	-	year	-12.40	1.0339	-	10.1	-	-	0.00476	-	-	0.00248	-
		N	10.10.06	o429	4	5.5	-7.87	0.05	0.05	-10.17	0.09	0.05	O.T.	-	year	-12.40	1.0332	-	12.9	-	-	0.00454	-	-	0.00363	-
				o430	4	8.5	-8.35	0.05	0.05	-9.42	0.07	0.05	O.T.	-	year	-12.40	1.0340	-	9.8	-	-	0.00491	-	-	0.00267	-
		P	11.15.06	o431	4	7.5	-7.47	0.09	0.05	-9.21	0.08	0.05	O.T.	-	year	-12.40	1.0343	-	8.9	-	-	0.00469	-	-	0.00291	-
				o572	2	3.7	-7.82	0.17	0.12	-8.90	0.18	0.11	O.T.	-	year	-12.40	1.0346	-	7.7	-	-	0.00485	-	-	0.00351	-
		R	12.12.06	o573*	4	3.6	-6.72	0.12	0.12	-8.75	0.17	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
				o574	2	4.0	-8.42	0.11	0.12	-8.96	0.19	0.11	O.T.	-	year	-12.40	1.0345	-	7.9	-	-	0.00550	-	-	0.00333	-
		T	01.16.07	o432	4	4.4	-7.77	0.15	0.05	-8.78	0.12	0.05	O.T.	-	year	-12.40	1.0347	-	7.2	-	-	0.00343	-	-	0.00350	-
		T	01.16.07	o575*	5	2.8	-7.45	0.17	0.12	-8.55	0.31	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		V	02.20.07	o433	5	6.7	-7.35	0.12	0.05	-8.42	0.11	0.05	3 m.	9.2	2 m.	-12.21	1.0349	2.88	6.6	-	-	-	-	-	-	-
				o434	4	7.9	-7.15	0.09	0.05	-9.33	0.09	0.05	3 m.	9.2	3 m.	-12.21	1.0339	1.95	10.2	-	-	-	-	-	-	-
				o435	4	8.4	-8.19	0.07	0.05	-8.61	0.09	0.05	3 m.	9.2	4 m.	-12.21	1.0347	2.68	7.3	-	-	-	-	-	-	-
		X	03.27.07	o436	4	5.6	-6.61	0.12	0.05	-9.30	0.17	0.05	3 m.	7.4	5 m.	-12.23	1.0340	1.59	10.0	2 m.	0.204	0.00345	0.0170	0.00490	0.00346	0.706
		Z	04.25.07	o437	4	6.1	-7.24	0.10	0.05	-8.23	0.15	0.05	3 m.	7.1	6 m.	-12.17	1.0350	2.57	5.9	2 m.	0.220	0.00463	0.0210	0.00481	0.00316	0.656
				o438	4	7.0	-7.74	0.07	0.05	-8.32	0.10	0.05	3 m.	7.1	7 m.	-12.17	1.0349	2.47	6.3	-	-	-	-	-	-	-
				o439	4	7.0	-8.17	0.09	0.05	-8.59	0.14	0.05	3 m.	7.1	8 m.	-12.17	1.0347	2.19	7.4	-	-	-	-	-	-	-
	A-1	A	04.07.06	o594	6	3.4	-7.69	0.14	0.12	-8.63	0.12	0.11	O.T.	-	year	-12.40	1.0349	-	6.6	-	-	0.00419	-	-	0.00308	-
		D	05.16.06	o590	2	1.5	-9.43	0.20	1.92	-8.02	0.29	0.19	O.T.	-	year	-12.40	1.0355	-	4.2	-	-	-	-	-	0.00319	-
		J	08.10.06	o591	3	2.0	-8.66	0.24	1.92	-9.68	0.37	0.19	O.T.	-	year	-12.40	1.0338	-	10.9	-	-	-	-	-	0.00323	-
		N	10.10.06	o496	12	7.2	-7.78	0.11	0.09	-10.24	0.08	0.05	2 w.	13.8	sampl.	-12.38	1.0332	2.25	13.2	sampl.	0.227	0.00596	0.0263	0.00425	0.00326	0.767
		P	11.15.06	o592	2	1.2	-7.53	0.27	1.92	-9.93	0.47	0.19	2 w.	13.2	sampl.	-12.26	1.0333	2.29	12.5	sampl.	-	-	-	0.00495	0.00312	0.630
		R	12.12.06	o497	15	8.2	-8.54	0.12	0.09	-9.42	0.10	0.05	2 w.	9.8	sampl.	-12.21	1.0338	2.01	10.6	sampl.	0.197	0.00649	0.0330	0.00496	0.00281	0.567
		T	01.16.07	o498	17	10.8	-8.09	0.11	0.09	-8.88	0.11	0.05	2 w.	7.3	sampl.	-12.23	1.0344	2.00	8.3	sampl.	0.204	0.00612	0.0300	0.00490	0.00255	0.519
		V	02.20.07	o499	8	5.2	-8.49	0.17	0.09	-9.34	0.12	0.05	O.T	-	year	-12.40	1.0341	-	9.5	-	-	0.00493	-	-	0.00259	-
		X	03.27.07	o593	6	2.0	-7.45	0.17	1.92	-8.86	0.28	0.19	O.T	-	year	-12.40	1.0346	-	7.6	-	-	-	-	-	0.00305	-
		Z	04.25.07	o500	14	10.7	-9.16	0.18	0.09	-8.69	0.17	0.05	O.T	-	year	-12.40	1.0348	-	6.9	-	-	0.00471	-	-	0.00303	-
	A-2	B	04.19.06	o608	12	3.2	-9.14	0.15	0.07	-8.72	0.14	0.05	O.T.	-	year	-12.4	1.0348	-	7.0	-	-	0.00458	-	-	0.00302	-
		D	05.16.06	o609	14	3.0	-8.35	0.18	0.09	-8.51	0.14	0.13	O.T.	-	year	-12.4	1.0350	-	6.2	-	-	0.00576	-	-	0.00304	-
		F	06.12.06	o610	4	1.3	-8.32	0.28	0.15	-8.71	0.32	0.06	O.T.	-	year	-12.4	1.0348	-	6.9	-	-	-	-	-	-	-
		H	07.11.06	o611	7	1.8	-8.62	0.36	0.15	-10.10	0.24	0.06	O.T.	-	year	-12.4	1.0333	-	12.6	-	-	-	-	-	-	-
		J	08.10.06	o564	28	11.4	-8.06	0.04	0.07	-10.25	0.07	0.07	3 m.	12.4	2 m.	-12.4	1.0332	1.99	13.0	2 m.	0.216	0.00571	0.0264	0.00430	0.00314	0.730
		L	09.12.06	o541	28	8.6	-8.26	0.08	0.07	-10.59	0.10	0.08	3 m.	13.9	2 m.	-12.4	1.0328	1.90	14.6	2 m.	0.208	0.00608	0.0292	0.00419	0.00260	0.621
		N	10.10.06	o542	28	10.8	-8.38	0.05	0.07	-10.48	0.07	0.08	3 m.	14.3	2 m.	-12.4	1.0329	2.13	14.2	2 m.	0.243	0.00610	0.0252	0.00486	0.00245	0.503
		P	11.15.06	o543	28	10.3	-7.93	0.08	0.07	-10.33	0.09	0.08	3 m.	14.7	2 m.	-12.3	1.0330	2.25	14.0	2 m.	0.242	0.00619	0.0256	0.00392	0.00261	0.666
		R	12.12.06	o544	28	10.0	-7.93	0.07	0.07	-10.34	0.12	0.08	3 m.	13.0	2 m.	-12.3	1.0329	1.86	14.1	2 m.	0.227	0.00656	0.0289	0.00425	0.00291	0.685
		T	01.16.07	o545	28	9.7	-7.96	0.08	0.07	-10.05	0.12	0.08	O.T.	-	year	-12.4	1.0334	-	12.4	-	-	0.00601	-	-	0.00275	-
		V	02.20.07	o546	22	6.2	-7.64	0.11	0.07	-9.87	0.05	0.07	O.T.	-	year	-12.4	1.0336	-	11.6	-	-	-	-	-	-	-
		X	03.27.07	o612	10	2.6	-8.28	0.11	0.09	-9.86	0.16	0.13	O.T.	-	year	-12.4	1.0336	-	11.6	-	-	0.00539	-	-	0.00298	-
		Z	04.25.07	o613	6	1.5	-8.00	0.28	0.15	-8.84	0.24	0.06	O.T.	-	year	-12.4	1.0346	-	7.5	-	-	-	-	-	-	-

Monthly averages

70	Ad	A	04.07.06	-7.65	0.06	0.06	-8.41	0.15	0.07	3 m.	4.8	1 m.	-12.64	1.0353	-	4.8	-	-	-	-	-	-	-
		B	04.19.06	-8.04	0.13	0.09	-7.98	0.24	0.09	3 m.	4.8	1 m.	-12.64	1.0358	-	3.2	2 m.	0.220	0.00411	0.0187	0.00367	0.00315	0.856
		D	05.16.06	-7.26	0.14	0.06	-7.96	0.16	0.07	3 m.	4.8	1 m.	-12.64	1.0358	-	3.1	2 m.	0.220	0.00473	0.0215	0.00367	0.00299	0.813
		F	06.12.06	-7.86	0.09	0.06	-8.03	0.08	0.07	3 m.	4.9	1 m.	-12.41	1.0355	-	4.2	-	-	-	-	-	-	-
		H	07.11.06	-9.67	0.15	0.06	-8.47	0.13	0.07	3 m.	5.1	1 m.	-12.58	1.0352	-	5.3	2 m.	0.211	0.00343	0.0162	0.00371	0.00308	0.830
		J	08.10.06	-9.01	0.09	0.06	-8.36	0.11	0.07	3 m.	5.3	1 m.	-12.33	1.0351	-	5.8	2 m.	0.213	0.00437	0.0205	0.00381	0.00309	0.812
		P	11.15.06	-7.66	0.11	0.06	-8.14	0.16	0.07	3 m.	5.7	1 m.	-12.34	1.0353	-	4.9	-	-	-	-	-	-	-
		R	12.12.06	-8.67	0.13	1.92	-8.25	0.29	0.19	3 m.	5.7	1 m.	-12.29	1.0351	-	5.6	-	-	-	-	-	-	-
		T	01.16.07	-7.70	0.14	0.06	-8.25	0.18	0.07	3 m.	5.7	1 m.	-12.28	1.0351	-	5.6	-	-	-	-	-	-	-
		V	02.20.07	-8.41	0.11	0.06	-8.19	0.12	0.07	3 m.	5.7	1 m.	-12.21	1.0351	-	5.6	2 m.	0.212	0.00376	0.0177	0.00375	0.00300	0.799
		X	03.27.07	-7.50	0.14	0.09	-8.15	0.18	0.09	3 m.	5.9	1 m.	-12.33	1.0353	-	5.0	2 m.	0.214	0.00486	0.0227	0.00454	0.00334	0.735
33	Ad	A	04.07.06	-8.48	0.09	0.06	-8.66	0.13	0.07	O.T.	-	year	-12.40	1.0348	-	6.8	-	-	0.00459	-	-	0.00299	-
		C	04.25.06	-8.61	0.16	0.12	-8.96	0.21	0.11	O.T.	-	year	-12.40	1.0345	-	7.9	-	-	0.00574	-	-	0.00327	-
		G	06.19.06	-8.69	0.13	0.12	-8.78	0.22	0.11	O.T.	-	year	-12.40	1.0347	-	7.2	-	-	-	-	-	-	-
		K	08.31.06	-4.22	0.23	0.12	-8.59	0.30	0.11	O.T.	-	year	-12.40	1.0349	-	6.5	-	-	-	-	-	-	-
		O	10.25.06	-8.44	0.11	0.12	-8.49	0.18	0.11	4 m.	7.2	1 m.	-12.31	1.0349	-	6.4	-	-	-	-	-	-	-
		Q	11.28.06	-8.18	0.10	0.06	-8.91	0.12	0.07	4 m.	7.6	1 m.	-12.38	1.0345	-	7.8	2 m.	0.216	0.00369	0.0171	0.00478	0.00296	0.619
		S	01.09.07	-7.94	0.10	0.06	-8.51	0.10	0.07	4 m.	7.9	1 m.	-12.31	1.0349	-	6.5	2 m.	0.216	0.00487	0.0225	0.00486	0.00270	0.556
		U	02.15.07	-8.68	0.13	0.06	-8.77	0.11	0.07	O.T.	-	year	-12.40	1.0347	-	7.2	-	-	-	-	-	-	-
		W	03.12.07	-7.38	0.10	0.06	-8.42	0.08	0.07	O.T.	-	year	-12.40	1.0351	-	5.8	-	-	-	-	-	-	-
		aa	05.01.07	-6.15	0.08	0.06	-8.21	0.11	0.07	O.T.	-	year	-12.40	1.0353	-	5.0	-	-	-	-	-	-	-
13	Ad	F	06.12.06	-7.46	0.07	0.05	-8.86	0.09	0.05	3 m.	6.9	2 m.	-12.54	1.0348	-	7.0	-	-	-	-	-	-	-
		H	07.11.06	-8.14	0.11	0.42	-9.05	0.12	0.08	O.T.	8.8	year	-12.40	1.0344	-	8.3	2 m.	0.212	0.00508	0.0240	0.00461	0.00322	0.697
		J	08.10.06	-7.98	0.06	0.05	-9.48	0.09	0.05	O.T.	-	year	-12.40	1.0340	-	10.0	-	-	0.00477	-	-	0.00275	-
		L	09.12.06	-7.37	0.07	0.05	-9.16	0.18	0.05	O.T.	-	year	-12.40	1.0343	-	8.8	-	-	0.00519	-	-	0.00270	-
		N	10.10.06	-8.11	0.05	0.05	-9.80	0.08	0.05	O.T.	-	year	-12.40	1.0336	-	11.3	-	-	0.00473	-	-	0.00315	-
		P	11.15.06	-7.65	0.13	0.09	-9.05	0.13	0.08	O.T.	-	year	-12.40	1.0344	-	8.3	-	-	0.00477	-	-	0.00321	-
		R	12.12.06	-8.42	0.11	0.12	-8.96	0.19	0.11	O.T.	-	year	-12.40	1.0345	-	7.9	-	-	0.00550	-	-	0.00333	-
		T	01.16.07	-7.77	0.15	0.05	-8.78	0.12	0.05	O.T.	-	year	-12.40	1.0347	-	7.2	-	-	0.00343	-	-	0.00350	-
		V	02.20.07	-7.56	0.09	0.05	-8.78	0.09	0.05	3 m.	9.2	2 m.	-12.21	1.0345	-	8.0	-	-	-	-	-	-	-
		X	03.27.07	-6.61	0.12	0.05	-9.30	0.17	0.05	3 m.	7.4	2 m.	-12.23	1.0340	-	10.0	2 m.	0.204	0.00345	0.0170	0.00490	0.00346	0.706
		Z	04.25.07	-7.72	0.09	0.05	-8.38	0.13	0.05	3 m.	7.1	2 m.	-12.17	1.0349	-	6.5	2 m.	0.220	0.00463	0.0210	0.00481	0.00316	0.656